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SYNOPSIS OF THE GENUS *ARABIS* (BRASSICACEAE) IN CANADA, ALASKA AND GREENLAND

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ABSTRACT

This taxonomic treatment of *Arabis* (Brassicaceae) in Canada, Alaska and Greenland recognizes 30 species. A comprehensive key is provided for these species and 8 varieties. Four new species are described: *A. boivinii* G. Mulligan, *sp. nov.*; *A. calderi* G. Mulligan, *sp. nov.*; *A. codyi* G. Mulligan, *sp. nov.*; and *A. murrayi,* G. Mulligan, *sp. nov.* In addition, many other taxa are recorded for the first time for this area. Cytological studies available for 45 North American and Greenland species of *Arabis* are summarized and discussed. Thirty-six of these species have the basic chromosome-number of $x = 7$ and some have diploid, triploid and even tetraploid chromosome races. The *Arabis* species being treated here can reproduce sexually and/or by agamospermy.

Key Words: Brassicaceae, *Arabis,* taxonomy, new species, cytology

INTRODUCTION

The first treatment of the genus *Arabis* in North America was on taxa in the Pacific Northwest (Rollins, 1936a). This was closely followed by two monographs published in *Rhodora*: *Arabis* in eastern and central North America by Hopkins (1937) and a monographic study of *Arabis* in western North America by Rollins (1941). Rollins discussed, in detail, the relationships of *Arabis* with other genera in the family Brassicaceae and among and within *Arabis* species. He continued to add to our knowledge of the taxonomy, ecology, cytology, breeding systems, hybridization and speciation in the genus in a long series of publications (Rollins, 1936a, 1936b, 1941, 1943, 1946, 1966, 1971, 1973, 1981, 1982,

1983, 1984, 1993a; Rollins and Rüdenberg, 1971, 1977, 1979). Böcher (1947, 1951, 1954, 1966, 1969) studied the cytology and embryology of some members of *Arabis* occurring in this area and Mulligan (1964) and Mulligan and Porsild (1969, 1970) published chromosome numbers for many *Arabis* taxa in Canada. Boivin (1951, 1955, 1967) also proposed a number of new taxa and rankings based on his study of Canadian *Arabis*. He summarized his taxonomic views on *Arabis* in his *Enumération des plantes du Canada* and *Flora of the Prairie Provinces* (Boivin, 1966, 1968, respectively). More recently, Sabourin (1989) presented a useful guide to the *Arabis* taxa found in eastern Canada. Rollins (1993b) published the first comprehensive taxonomic study of the genus *Arabis* in Continental North America. He included excellent keys, descriptions, habitats, distributions, and cytological data for all taxa based on material that he had seen. However, he did not have the opportunity to see the large amount of Canadian, Alaskan and Greenland *Arabis* material available to me. Consequently, many *Arabis* taxa present in Canada, Alaska and Greenland are not recorded from this area in Rollins' latest treatment. The present synopsis of *Arabis* occurring in Canada, Alaska and Greenland attempts to fill this gap.

MATERIALS AND METHODS

Herbarium specimens, including many types, were examined morphologically. They were borrowed from the following institutions: ALA, CAN, DAO, DWC, GH, K, KY, LE, MO, MT, ND, NY, ORE, OS, P, PH, QFA, RM, RSA, SASK, UBC, UC, US, WIS and WS. Herbarium acronyms are according to Holmgren et al. (1990). In addition, a very large collection of unmounted, mostly unidentified, *Arabis* specimens were studied and later deposited in the herbarium of Agriculture Canada, Ottawa (DAO). These specimens were collected in southwestern Canada and the western United States by Theodore Mosquin, with Linda Mosquin and M. H. Benn in 1962 and with G. A. Mulligan and J. M. Gillett in 1963. Many of these specimens had both herbarium labels and annotation slips containing unpublished cytological data of Theodore Mosquin. In addition, cytological studies published for all North American and Greenland species of *Arabis* were summarized. The cytological information appears in Table 1.

CYTOLOGY AND BREEDING SYSTEMS

Results from the cytological examination of 45 species of *Arabis* of North America and Greenland are presented in Table 1. Thirty-six species have the base chromosome-number of $x = 7$, eight species have $x = 8$, and one species, *A. glabra,* seems to have two base numbers, $x = 6$ and 8.

Nineteen of the species with the base number of $x = 7$ are known only as diploids, five species only as triploids, one species only as a tetraploid, nine species as both diploids and triploids, and two species as diploids, triploids and tetraploids. Seventeen of these thirty-six species, with the base number of $x = 7$, contain plants that are triploid and/or have an irregular meiosis. Since these plants have almost a complete seed set, it seems likely that they produce seed by apomixis. Eight species (*A. columbiana, A. divaricarpa, A. drummondii, A. exilis, A. holboellii, A. laevigata, A. puberula* and *A. sparsiflora*), also with a very high seed set, have plants with a regular pairing at meiosis and thus may very well be sexual. However, all of these eight species also have plants that are triploid and/or have an irregular meiosis and thus are almost certainly also apomictic. A number of species, with the base number of $x = 7$, include aneuploids and plants with B-chromosomes.

Böcher (1947, 1951, 1954, 1966, 1969) first reported apomixis in North American and Greenland *Arabis* with the base number of $x = 7$. According to Böcher (1969), some diploids with a completely normal meiosis seem to be sexual whereas others with meiotic abnormalities are probably apomictic or amphi-apomictic. He also stated that triploids may easily be formed by the fusion of reduced and unreduced cells in diploids and that this process may be reversible. The most common base number for North American and Greenland *Arabis* is $x = 7$, and these species may be sexual, apomictic or amphi-apomictic or any combination thereof. It appears that plants with the base number $x = 7$, some possibly propagating apomictally, do occur occasionally on other continents. For example, Berkutenko and Gurzenkov (1976) reported $2n = 14$ for *Arabis falcata* (Turcz.) Berkut. and $2n = 21$ for *Arabis pendula* L. from the south Magadan region in the former U.S.S.R. and Galland (1969) $2n = 14$ for plants of *Arabis auriculata* Lam. and *Arabis conringioides* Ball. from Morocco. *Arabis pauciflora* (Grimm.) Garcke has the chromosome number of $2n$

Table 1. Reported chromosome-numbers for *Arabis* of Canada, the United States and Greenland. Chromosome counts and other cytological information attributed to voucher specimens under the collection numbers of Theodore Mosquin (T.M.) were observed by him and were attached to specimens that are now deposited in the Agriculture Canada herbarium at Ottawa (DAO). The references given in Table 1 refer to published reports. The chromosome numbers listed as $n = 15/2$, 21/2, and 22/2 indicate that Mosquin observed very irregular configurations totalling 15, 21 and 22 chromosomes, respectively, at meiosis.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
A. aculeolata Greene		32	OREGON (Rollins & Rüdenberg 1977).
A. alpina L.	8	16	GREENLAND (Jörgensen *et al.* 1958; Dalgaard 1988, 8II). QUEBEC (Rollins 1941; Mulligan 1964). MANITOBA (Löve & Löve 1982).
A. arenicola (Richardson) Gelert	8	16	GREENLAND (Böcher 1966). QUEBEC (Hedberg 1967; *Lepage 39394* by T.M.).
A. boivinii G. Mulligan	21/2		MONTANA (*T.M. & L. Mosquin 5219*). SOUTH DAKOTA (*T.M. & G.A. Mulligan 5157*).
A. breweri S. Wats.		14	CALIFORNIA (Rollins & Rüdenberg 1971).
A. canadensis L.		14	ONTARIO (Mulligan 1964).
A. caucasica Willd.	8		ONTARIO (Mulligan 1964, 8II).
A. cobrensis M.E. Jones	7		WYOMING (Rollins 1941).
A. columbiana Macoun	7		BRITISH COLUMBIA (*T.M. & G.A.M. 4930 & 4937*, meiosis irregular). CALIFORNIA (*T.M. 4548*). IDAHO (*T.M. & G.A.M. 4966, 4982 & 4994*, meiosis irregular; *T.M. & G.A.M. 4998*, 7II). OREGON (*T.M. & G.A.M. 4953*, 7II).
	21/2	*ca.* 21	CALIFORNIA (*T.M. 4531 & 4535*). WASHINGTON (*T.M. & G.A.M. 4944*, $n = 21/2$).

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
	22/2		WASHINGTON (*T.M. & G.A.M. 4946*).
A. constancei Rollins		14	CALIFORNIA (Rollins & Rüdenberg 1971).
A. crandallii Robinson	7	14	COLORADO (Rollins 1941, 1966).
A. demissa var. *russeola* Rollins		21	WYOMING (Rollins 1966).
A. depauperata Nelson & Kennedy	7		MONTANA (*T.M. & J.M. Gillett 5253*).
A. divaricarpa A. Nels. var. *divaricarpa* or *dacotica* (Greene) Boivin	7	14	MANITOBA (Löve & Löve 1975a, 1982). COLORADO (Rollins 1966). MONTANA (Rollins 1966, 1983).
		22	CALIFORNIA (Rollins 1966). WYOMING (Böcher 1969, apomictic, EMCs, PMCs, and pollen grains had 22 chromosomes and dyads and uniform pollen were formed). The $n = 8$ and $n = 15$ chromosome-number reports by L.O. Gaiser in Rollins (1941) are probably erroneous (Rollins, pers. comm.).
A. divaricarpa var. *divaricarpa*	7	14	SASKATCHEWAN (Taylor & Brockman 1966). ALBERTA (*T.M., L.M. & M.H. Benn 4751 & T.M. & L.M. 4703*, 7II). BRITISH COLUMBIA (Mulligan 1964, $2n = 13 + 2B$ & 14). COLORADO (*T.M. & L.M. 4575*).
	15/2		MONTANA (*T.M. & J.M.G. 5258*).
	21/2	21	ALBERTA (*T.M. & M.H.B. 5183*, $n = 21/2$). BRITISH COLUMBIA (Mulligan 1964). CALIFORNIA (*T.M. 4529*).
A. divaricarpa var. *dacotica*	*ca.* 7		COLORADO (*T.M. & L.M. 4575*)
	21/2	21	BRITISH COLUMBIA (Mulligan 1964). COLORADO (T.M. & G.A.M. 5066 & 5073, $n = 21/2$).

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
	14	28	MACKENZIE DISTRICT (Mulligan 1964, 2*n* = 28 & 28 + 1B). MANITOBA (*T.M. & L.M. 4904 & 4910,* *n* = 14 with irregular meiosis).
A. drummondii Gray	7	14	YUKON (Mulligan 1964). MANITOBA (Löve & Löve 1982). ALBERTA (*T.M. & L.M. 4706 & T.M., L.M. & M.H.B. 4737,* both 7II). CALIFORNIA (Rollins & Rüdenberg 1977). COLORADO (Rollins 1941, 1966; Rodman & Bhargava 1976; *T.M. & L.M. 4580, 4616 & 4630,* all 7II; *T.M. & G.A.M. 5068, 5093 & 5101,* all 7II). IDAHO (*T.M. & G.A.M. 4999*). MONTANA (Rollins 1966, 1983; *T.M. & J.M.G. 5232, 5232a & 5260,* all 7II). UTAH (*T.M. & G.A.M. 5120,* 7II). WYOMING (Rollins 1966, 1983; *T.M. & L.M. 4658, 4663 & 4668,* all 7II; *T.M. & J.M.G. 5246 & 5247,* both 7II).
		20	BRITISH COLUMBIA (Mulligan 1964).
	21/2	21	ALBERTA (*T.M. & L.M. 4755,* 7II + 7I; *T.M. & M.H.B. 4738*).
	14	28	MASSACHUSETTS (Böcher 1969).
A. eschscholtziana Andrz.	32		BRITISH COLUMBIA (Taylor & Mulligan 1968, 32II).
A. exilis A. Nels.	7	14	YUKON (Böcher 1969). BRITISH COLUMBIA (Mulligan 1964; Taylor & Taylor 1977, 7II). MONTANA (Böcher 1969). WYOMING (Rollins 1966; Böcher 1969).
		ca. 21	UTAH (*T.M. & G.A.M. 5122*).

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
A. fendleri (S. Wats.) Greene	7	14	CALIFORNIA (Rollins & Rüdenberg 1979). COLORADO (Rollins 1941, 1966). The *n* = 14 report for Colorado material in Rollins (1941) may be erroneous (Rollins, pers. corr.).
		21	NEVADA (Rollins & Rüdenberg 1979). The *n* = 21 report for Colorado material in Rollins (1941) is almost certainly erroneous.
A. glabra (L.) Bernh.	6	12	QUEBEC (*Gillett 10569*, 2*n* = 12 by T.M.). ONTARIO (*Bowden*, 2*n* = 12 by G.A.M.). ALBERTA (*T.M. & L.M. 4687*). CALIFORNIA (*T.M. 4542, 4515B & 4815*, all 6II; *Breedlove*, 6II by T.M.). COLORADO (Rodman & Bhargava 1976; *T.M. & G.A.M. 5104*, 6II). IDAHO (*T.M. 4795*). MONTANA (*T.M. & J.M.G. 5218*, meiosis regular). OREGON (*T.M. & L.M. 4359 & 4484*, 6II). WYOMING (*T.M. & L.M. 4669* 6II).
	8		VIRGINIA (Hill 1982).
A. glaucovalvula M.E. Jones	7		CALIFORNIA (Rollins & Rüdenberg 1979).
A. gunnisoniana Rollins	7		COLORADO (Rollins 1941).
A. hirsuta (L.) Scop. var. *hirsuta*	16		CALIFORNIA (*T.M. 4525*, 16II). COLORADO (*T.M. & J.M.G. 5347*, 16II).
A. hirsuta var. *pycnocarpa* (Hopkins) Rollins	16	32	MACKENZIE DISTRICT (Mulligan 1964). MANITOBA (Taylor & Brockman 1966). ALBERTA (*T.M. & L.M. 4688 & 4701*, 16II; *T.M. & M.H.B. 5184*, 16II). BRIT-

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
			ISH COLUMBIA (*T.M. & G.A.M. 4933,* 16II). CONNECTICUT (Rollins 1941). COLORADO (Rollins 1941). SOUTH DAKOTA (*T.M. & G.A.M. 5154 & 5155,* 16II). WISCONSIN (Smith 1938, 16II). The *n* = 32 chromosome-number by L.O. Gaiser in Rollins (1941) should be discounted until it is confirmed.
A. holboellii Hornem. var. *holboellii*	7	14	GREENLAND (Böcher 1954; Böcher 1969, some have completely normal meiosis and seem to be sexual whereas others probably are amphiapomictic or apomictic; Dalgaard 1988, 7II).
		21	GREENLAND (Böcher 1954; Böcher 1969, metaphases correspond to those of second division, PMCs have asyndetic metaphase plates with the somatic number; *Hansen et al. 2304,* 2*n* = *ca.* 21 by T.M.).
A. holboellii var. *consanguinea* (Greene) G. Mulligan	7		NEVADA (*T.M. & L.M. 4335 & 4337,* 7II).
	21/2	21	ALBERTA (*T.M. & L.M. 4696 & 4705*; *T.M. 5201,* *n* = *ca.* 21/2, meiosis irregular; *T.M. & M.H.B. 5212,* *n* = *ca.* 21/2). CALIFORNIA (*T.M. & P. Raven 4419*; *T.M. & L.M. 4440 & 4441,* *n* = 21/2). COLORADO (*T.M. & L.M. 4623*; *T.M. & G.A.M. 5094*). OREGON (*T.M. & L.M. 4485*; *T.M. & J.M.G. 5276*).

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
A. holboellii var. *retrofracta* (Graham) Rydb.	7	14	MANITOBA (Mulligan 1964; Löve & Löve 1982; *T.M. & L.M. 4911,* 7II). SASKATCHEWAN (Mulligan 1964; *T.M. & L.M. 4914 & 4915,* both 7II). ALBERTA (Mulligan 1964; *T.M. & L.M. 4683 & 4686,* both 7II; *T.M. & G.A.M. 4924,* 7II). BRITISH COLUMBIA (Mulligan 1964; *T.M. & L.M. 4454 & 4460,* both 7II; *J.A. Calder & J.M.G. 26537,* 7II by T.M.; *T.M. & G.A.M. 4935 & 4938,* both 7II; *T.M. & G.A.M. 4929, n* = 7, meiosis irregular). CALIFORNIA (Rollins 1941, 1966; Rollins & Rüdenberg 1977; *T.M. & P. Raven 4427,* 7II; *T.M., 4532*; *T.M. 4530, n* = 7 meiosis irregular). COLORADO (Rollins 1941; *T.M. & L.M. 4628,* 7II). IDAHO (Böcher 1969, meiosis regular with 7 bivalents, hundreds of anaphase I were normal, only tetrads were formed and pollen was uniform; *T.M. & G.A.M. 4967, 4970, 4972, 4997 & 4998,* all 7II). MONTANA (Rollins 1966, 1983). NEVADA (*T.M. & G.A.M. 5001 & 5008,* both 7II; *T.M. & G.A.M. 5013, n* = 7, irregular meiosis). OREGON (*T.M. & G.A.M. 4962,* 7II). SOUTH DAKOTA (*T.M. & G.A.M. 5151, n* = 7, irregular meiosis). WASHINGTON (Böcher 1969). WYOMING Rollins 1941, 1983; Böcher 1969; *T.M. & L.M. 4665,* 7II).
	14 + 1B		ALBERTA (Packer 1964). BRITISH COLUMBIA (Mulligan 1964).

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
	15/2		ALBERTA (*T.M., L.M. & M.H.B. 4735*, 7II +1I). BRITISH COLUMBIA (*T.M. & G.A.M. 4932*). COLORADO (*T.M. & G.A.M. 5097*, irregular meiosis).
	ca. 21/2	21	ALBERTA (*T.M. & G.A.M. 4922*, *n* = *ca.* 21/2). BRITISH COLUMBIA (*T.M. & L.M. 4452*, *n* = *ca.*21/2, meiosis irregular). IDAHO (*T.M. & L.M. 4156*, *n* = *ca.* 21/2, PMCs form dyads not tetrads). OREGON (*T.M. & L.M. 4353*). WYOMING (*T.M. & L.M. 4164*, *n* = 21/2). The *n* = 14 chromosome-number given in Rollins (1941) may be erroneous.
A. holboellii var. *secunda* (Howell) Jepson	7	14	QUEBEC (Böcher 1954). IDAHO (*T.M. & G.A.M. 4983*, 7II).
		21	BRITISH COLUMBIA (Mulligan 1964).
			UTAH (*T.M. & G.A.M. 5119*).
	ca. 22/2		UTAH (*T.M. & G.A.M. 4988*).
A. inyoensis Rollins		21	NEVADA (Rollins & Rüdenberg 1971).
		23	NEVADA (Rollins & Rüdenberg 1971).
A. kamtschatica (Fisch.) Ledeb.		32	ALASKA (Dawe & Murray 1979, 2*n* = 32 as on voucher in ALA not 2*n* = 16 as in paper; Rollins 1966, under *A. lyrata*). YUKON (Mulligan 1964, under *A. lyrata*). BRITISH COLUMBIA (Taylor & Mulligan 1968, Mulligan 1964, under *A. lyrata*). The GH voucher for *A. lyrata* ssp. *kamtschatica* of Johnson & Packer 1968 is *A. media*.

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
A. laevigata (Mühl) Poir.		7	CONNECTICUT (Rollins 1941). MARYLAND (Kovanda 1978). OHIO (Easterly 1963, 7II). WISCONSIN (Smith 1938, 7II).
A. lemmonii S. Wats.		14	ALBERTA (Mulligan 1964). BRITISH COLUMBIA (Mulligan 1964). WYOMING (Rollins 1966).
	ca. 21/2		MONTANA (*T.M. & J.M.G. 5229 & 5252*).
A. lignifera A. Nels.	7	14	COLORADO (Rollins 1941). WYOMING (Rollins 1941).
A. lyallii S. Wats.	21/2	21	ALBERTA (Mulligan 1964). BRITISH COLUMBIA (Mulligan 1964). UTAH (*T.M. & J.M.G. 5322, n* = 21/2).
A. lyrata L.	8	16	ONTARIO (Böcher 1969; *Garton 6191,* 8II by T.M.).
A. media N. Busch		16	ALASKA (Rollins 1966 under *A. lyrata* but voucher in GH is *A. media*); Johnson & Packer 1968 under *A. lyrata* subsp. *kamtschatica* but voucher in GH is *A. media*).
A. microphylla Nuttall	7	14	BRITISH COLUMBIA (Mulligan 1964). OREGON (Rollins 1941).
	15/2	15	WYOMING (Böcher 1969, PMCs form dyads and anaphases initiating dyads were all regular with 15 chromosomes). The *n* = 14 chromosome-number in Rollins (1941) may be erroneous.
A. parishii S. Wats.	7		CALIFORNIA (Rollins & Rüdenberg 1979).

Table 1. Continued.

Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
A. pendulina Greene	7	14	UTAH (Böcher 1969, pollen was uniform).
A. perennans S. Wats.	7	14	COLORADO (Rollins 1941). ARIZONA (Rollins & Rüdenberg 1971).
A. perstellata Braun	7		TENNESSEE (Rollins 1966).
A. petiolaris (Gray) Gray	14	*ca.* 28	TEXAS (Rollins & Rüdenberg 1977).
A. pinetorum Tidestrom	7	14	ALASKA (Dawe & Murray 1979 under *A. holboellii* but voucher in ALA is *A. pinetorum*). CALIFORNIA (*T.M. 4547*, *n* = 7, meiosis irregular).
		13 + 2B	MANITOBA (Mulligan 1964 under *A. holboellii*).
	21/2	21	CALIFORNIA (*T.M. & L.M. 4439*; Rollins & Rüdenberg 1971). NEVADA (*T.M. 4536*). WYOMING (Rollins 1966).
A. puberula A. Nels.	7		NEVADA (*T.M. & L.M. 4337*, 7II).
	21/2		OREGON (*T.M. & L.M. 4347 & 4349*).
A. pulchra M.E. Jones	7	14	NEVADA (Rollins & Rüdenberg 1979). UTAH (Rollins & Rüdenberg 1971).
		21	NEVADA (Rollins & Rüdenberg 1979). UTAH (Rollins & Rüdenberg 1971).
A. repanda S. Wats.	7		CALIFORNIA (Rollins 1941).
A. schistacea Rydb.		14	UTAH (Böcher 1969, pollen is uniform).
A. selbyi Rydb.		*ca.* 21	COLORADO (Rollins & Rüdenberg 1977).

Table 1. Continued.

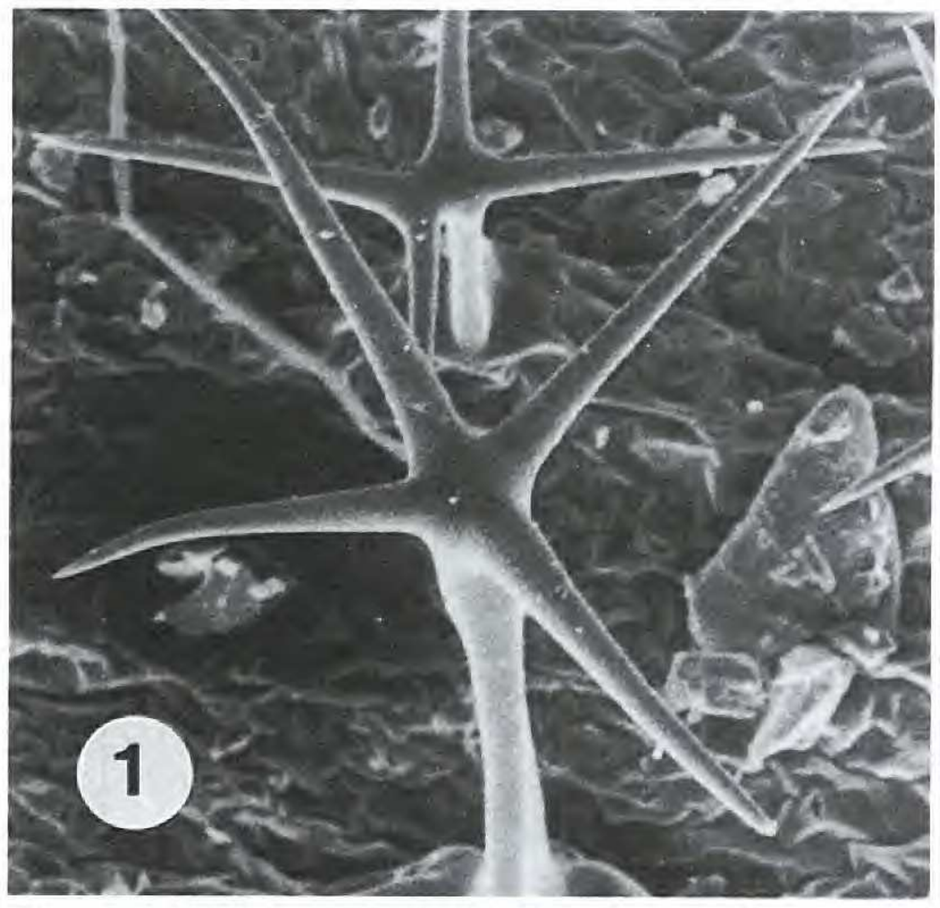
Taxon	*n*	2*n*	Sources of materials, vouchers or references, and special cytological information
A. serotina Steele		14	VIRGINIA (Wieboldt 1987).
A. sparsiflora Nuttall	7		ARIZONA (*T.M. & L.M. 4245*, meiosis irregular). IDAHO (*T.M. & L.M. 4338 & 4352*, both 7II).
	22/2	22	CALIFORNIA (Raven *et al.* 1965; Böcher 1969, 7II + 8I at metaphase I).
A. subpinnatifida S. Wats.		7	OREGON (Rollins & Rüdenberg 1977).

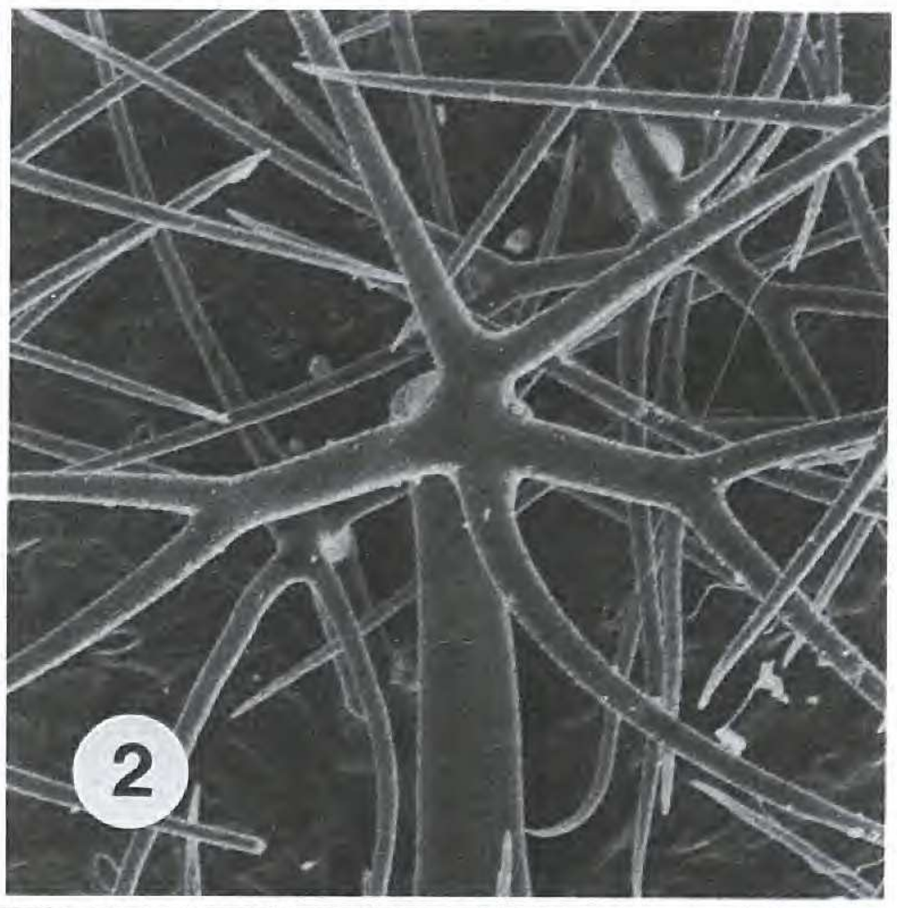
= 14 in Austria, Sweden, France and Germany (Burdet, 1967). However, he does not think that it is related to North American *Arabis* with the base number $x = 7$. He points out that this species has baffled European taxonomists, who have placed it at various times in the genera *Turritis, Brassica, Conringia* and even *Erysimum.*

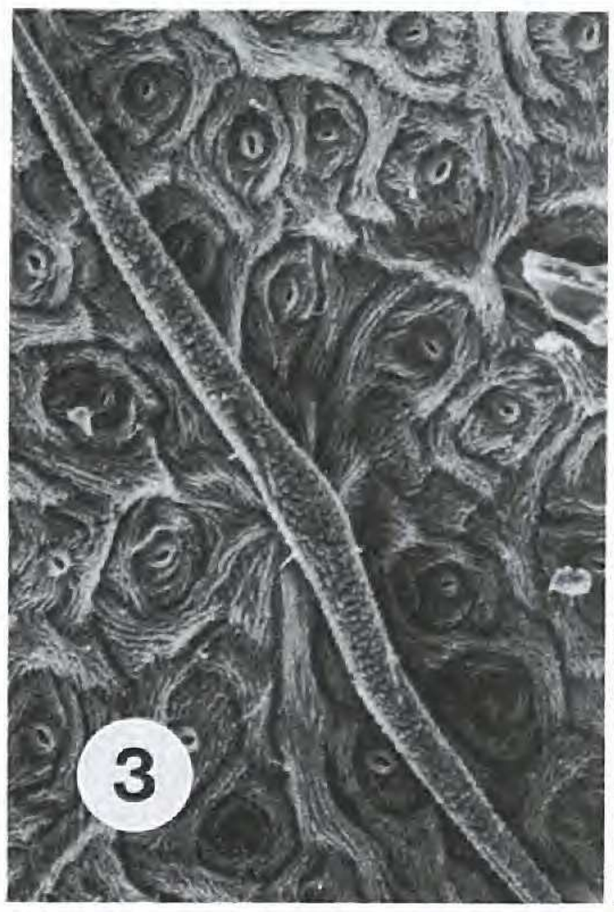
The eight North American species of *Arabis* with the base number of $x = 8$, and *A. glabra,* with $x = 6$ and 8, all appear to produce seed sexually. All of the material, with these base numbers, examined by the author and by other workers on North American material and plants from continents, had a regular meiosis and/or lacked triploids, and, with the exception of *A. caucasica,* had a very high seed set when found growing in isolation. They are, therefore, almost certainly sexual and self-compatible. Burdet (1967) considers $x = 8$ to be the common basic chromosome-number of European and Asiatic *Arabis.* He does suggest that the base number may even be $x = 4$ because of chromosome-counts of $2n = 8$ for plants of *A. hirsuta* from Switzerland and France. Burdet (1967) states that the somatic chromosomes of *A. glabra* are quite different from those of other *Arabis,* supporting other evidence that it perhaps could be placed in another genus.

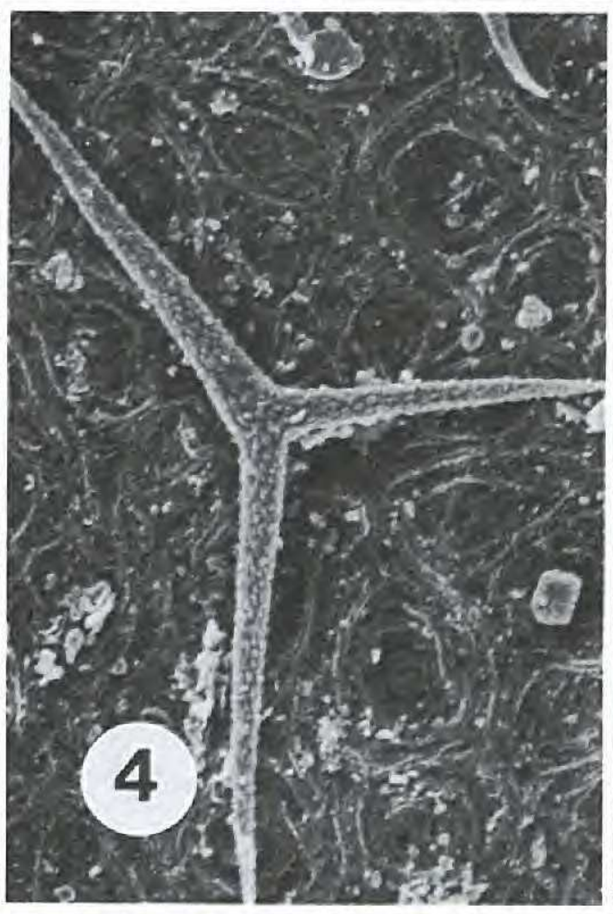
TRICHOMES IN *ARABIS*

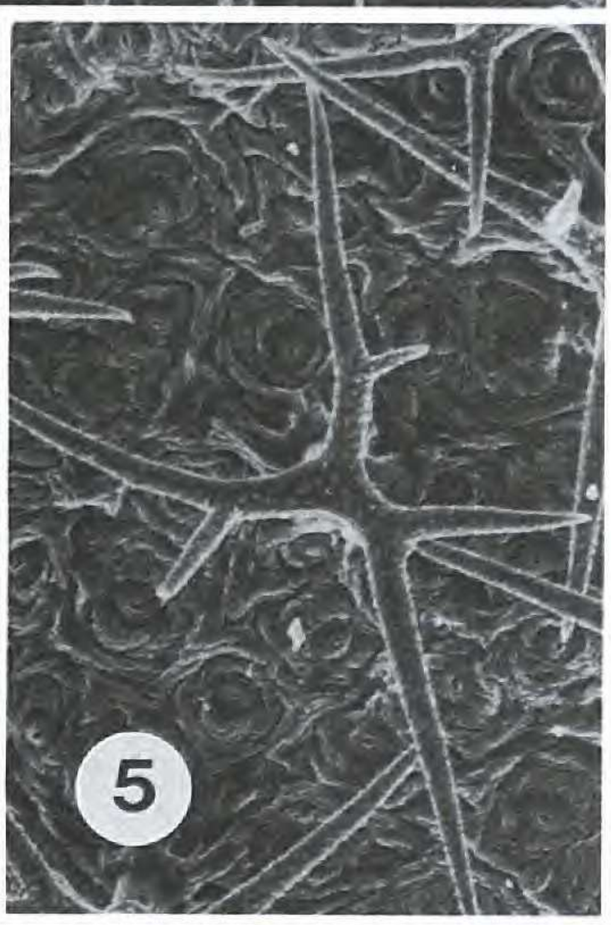
The trichomes on the undersurfaces of the caudex leaves, when present, often differ from taxon to taxon. They vary from simple or once-forked to dendritic or stellate and the more complex ones are from sessile to long-stalked. Scanning electron microscope (SEM) photographs of the more complex trichomes are shown in Figures 1 to 20. Where the trichomes are similar, a close relationship may be indicated. This seems to be the case for *A. drummondii, A. calderi, A. lyallii, A. divaricarpa* var. *divaricarpa* and *A. divaricarpa* var. *dacotica* (Figures 3 to 7, respectively). In most cases, the trichomes are very different in form and/or size; for example *A. caucasica* (Figure 2), *A. microphylla* (Figure 13), *A. sparsiflora* (Figure 18) and *A. pinetorum* (Figure 20). These differences in the morphology and size of trichomes on the undersurfaces of the caudex leaves have been used extensively in the key to separate taxa.

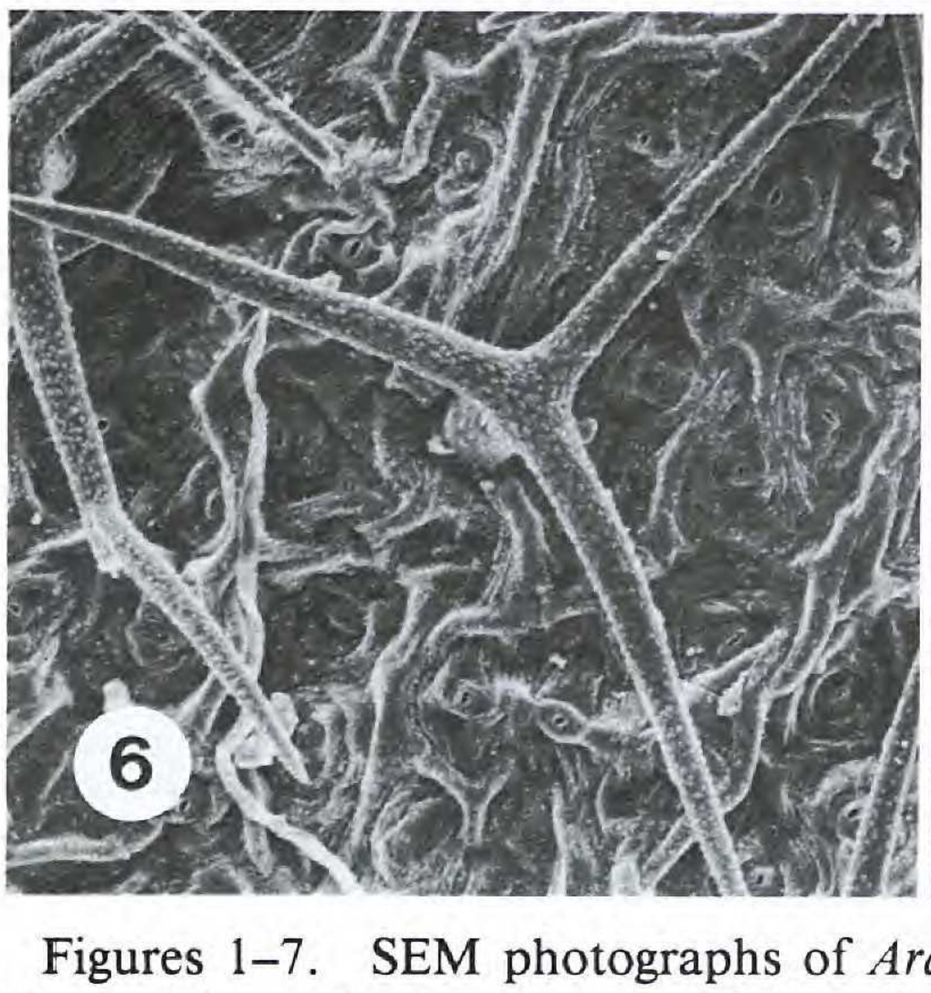


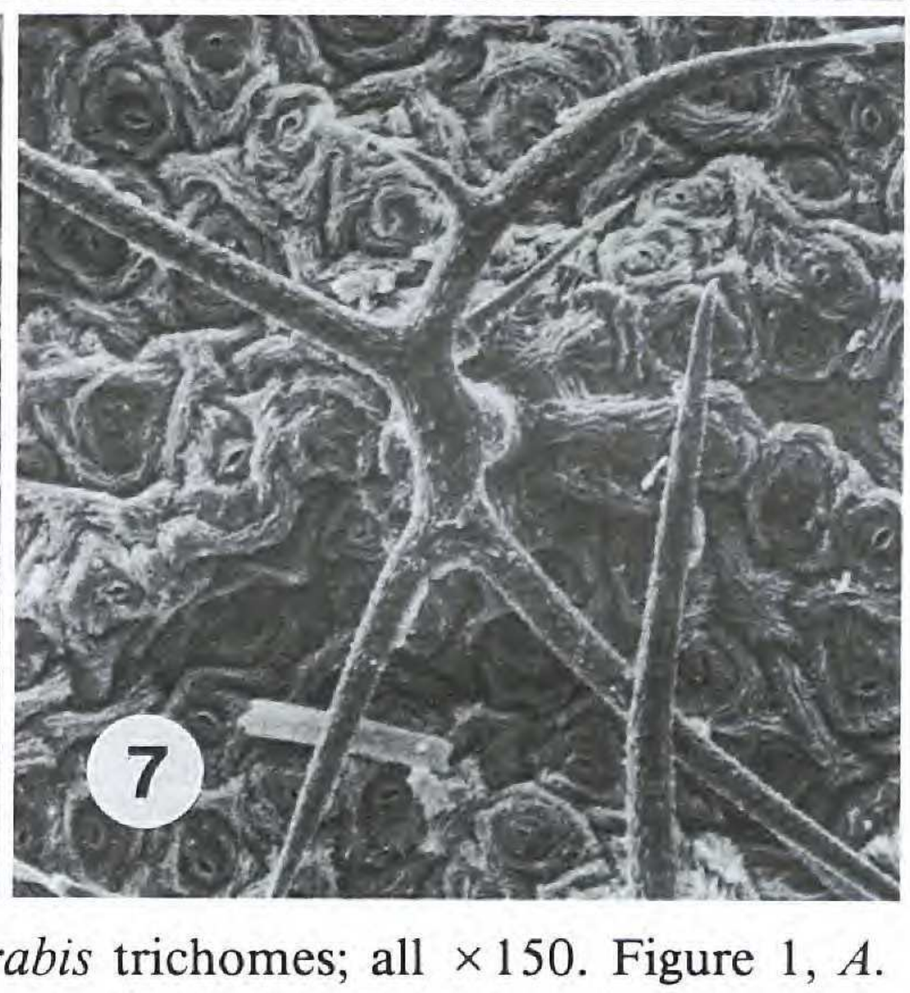












Figures 1–7. SEM photographs of *Arabis* trichomes; all ×150. Figure 1, *A. alpina.* Figure 2, *A. caucasica.* Figure 3, *A. drummondii.* Figure 4, *A. calderi.* Figure 5, *A. lyallii.* Figure 6, *A. divaricarpa* var. *divaricarpa.* Figure 7, *A. divaricarpa* var. *dacotica.*

TAXONOMIC TREATMENT

KEY TO TAXA OF *ARABIS* OF CANADA, ALASKA AND GREENLAND

1. Bases of middle cauline leaves all attenuate, cuneate, obtuse, to truncate, never clasping stems 2
   2. Siliques strongly descending to pendulous 3
      3. Stems 3 to 9 dm high; biennials, usually lacking caudex leaves as plants mature; caudex leaves, if present, glabrous or with simple to once-branched trichomes to 0.5 mm long; siliques 2.0 to 3.25 mm wide; seeds prominently winged; sw Que., s Ont., and southward ..... **11.** *A. canadensis*
      3. Stems usually less than 3 dm high; perennials with persistent caudex leaves; surfaces of caudex leaves with short-stalked (less than 0.063 mm long) semistellate trichomes mostly 0.125 mm wide; siliques 1.5 to 2.0 mm wide; seeds only slightly winged; Yukon, Sask. (Cypress Hills), sw Alta., B.C., and southward ..... **22.** *A. exilis*
   2. Siliques ascending to erect 4
      4. Siliques strongly ascending to erect; surfaces of caudex leaves glabrous or with short-stalked (less than 0.063 mm long) semidendritic to dendritic trichomes mostly 0.125 mm wide; sw Yukon, s B.C., and southward ..... **21.** *A. murrayi*
      4. Siliques ascending; surfaces of caudex leaves with simple or medium- to long-stalked (0.063 mm long or longer) 1- to 2-branched, -forked or -rayed trichomes from 0.25 to 1.5 mm long or wide 5
         5. Some caudex leaf blades with a larger terminal segment and two to many much smaller lateral segments or prominent lobes 6
            6. Petals 6.0 to 8.0 mm long; siliques 0.75 to 1.0 mm wide; beaks of siliques 0.5 to 1.0 mm long, much longer than wide; surfaces of caudex leaves with few to many simple trichomes 0.75 to 1.25 mm long; larger terminal segments of caudex leaves usually ovate; Ont., Man., Sask., Alta., and southward ..... **4.** *A. lyrata*

6. Petals (4.0) 5.0 to 5.5 mm long; siliques 1.25 to 1.5 mm wide; beaks of siliques usually less than 0.5 mm long, shorter to slightly longer than wide; surfaces of caudex leaves usually glabrous, rarely with few to scattered 2-forked or -rayed trichomes to 0.75 mm long; larger terminal segments of caudex leaves usually broadly ovate to orbicular; Alaska, westward into Russia, Yukon, Mack. Dist., n Sask., sw Alta., B.C., and Wash. ..... **5.** *A. kamtschatica*

5. All caudex leaf blades entire, sparingly toothed or with one to few pairs of shallow to deep lobes; none of leaf blades with a larger terminal segment and smaller lateral segments or prominent lobes 7

7. Petals (4.5) 7.0 to 8.0 mm long; outer sepals prominently saccate at base; surfaces of caudex leaves mostly with simple trichomes 0.75 to 1.5 mm long; Yukon (rare), sw Alta., se B.C., and southward ..... **10.** *A. nuttallii*

7. Petals 4.0 to 5.5 mm long; outer sepals weakly saccate; surfaces of caudex leaves glabrous or mostly with branched or rayed trichomes less than 0.75 mm long or wide 8

8. Siliques subterete with prominent midvein from base to apex, 0.75 to 1.0 (1.25) mm wide; surfaces of caudex leaves mostly with medium-stalked (0.063 to 0.125 mm long) 2- to 3-rayed trichomes; n Alaska, westward into Russia, and n Yukon ..... **2.** *A. media*

8. Siliques flattened, prominent midvein absent towards apex, 1.5 to 2.5 (3.0) mm wide; surfaces of caudex leaves glabrous or with simple and long-stalked (over 0.125 mm long) branched or rayed trichomes 9

9. Plants glabrous, except for occasional simple trichomes on leaf margins; Mack. Dist., Keew. Dist., Frank. Dist., Greenland, Labrador, n Que., n Ont., and n Sask. ..... **3a.** *A. arenicola* var. *arenicola*

9. Plants with copious simple, 1- to 2-branched and long-stalked 2-rayed trichomes on stem and leaf surfaces; Keew. Dist., n Que., n Ont., n Man., and n Sask. ..... **3b.** *A. arenicola* var. *pubescens*

1. Bases of middle cauline leaves always auriculate-, hastate-, to sagittate-clasping stems 10
10. Caudex leaves glabrous, or absent when plants mature 11
11. Siliques erect-appressed to rachis 12
12. Siliques subterete; petals yellow, about as long as sepals; biennials with basal leaves few or absent as plants mature; bases of stems with spreading trichomes; Alaska, Yukon, Mack. Dist., Que., Ont., Man., Sask., Alta., B.C., southward, Europe, and Asia ..... *A. glabra*
12. Siliques strongly flattened; petals whitish to purplish, about twice as long as sepals; short- to long-lived perennials with caudex leaves persisting as plants mature; bases of stems glabrous or with malpighiaceous trichomes; Alaska, Yukon, Mack. Dist., Nfld., N.S., N.B., Que., Ont., Man., Sask., Alta., B.C., and southward ..... **14.** *A. drummondii*
11. Siliques descending, spreading, ascending to strongly ascending 13
13. Inflorescences secund; Yukon (rare), w Alta., B.C., and southward ..... **18.** *A. lemmonii*
13. Inflorescences symmetrical 14
14. Siliques strongly ascending, (2.0) 2.25 to 3.5 mm wide; stems 1.0 to 2.5 (4.0) dm high; persistent perennials with much branched, many-stemmed, caudexes; sw Alta., s B.C., and southward ..... **16.** *A. lyallii*
14. Siliques descending, spreading to ascending, 0.75 to 2.0 mm wide; stems (2) 3 to 10 dm high; biennials or short-lived perennials with basal leaves often absent as plants mature; single to few stemmed 15
15. Siliques up to 25 mm long and 0.75 mm wide, with a scattered simple to once-forked puberulence; petals up to 2.0 mm long; Essex Co. Ont., and southward ..... **13.** *A. shortii*
15. Siliques more than 25 mm long and 0.75 mm wide, glabrous, petals longer than 2.0 mm 16

16. Cauline leaves more than 10 mm wide; basal leaves usually absent; siliques spreading and strongly downwardly arcuate; sw Que., s Ont., and southward ..... **12.** *A. laevigata*

16. Cauline leaves mostly less than 10 mm wide; basal leaves mostly persisting; siliques descending, spreading to ascending, straight to slightly arcuate; Alaska (rare), Yukon, Mack. Dist., Que., N.B. (rare), Ont., Man., Sask., Alta., B.C., and southward ..... **17a.** *A. divaricarpa* var. *divaricarpa*

10. Caudex leaves present and hairy 17

17. Surfaces of caudex leaves with simple trichomes only; siliques spreading and strongly downwardly arcuate; sw Que., s Ont., and southward ..... **12.** *A. laevigata*

17. Surfaces of caudex leaves with some forked or rayed trichomes; if siliques are spreading and strongly downwardly arcuate, the trichomes on surfaces of caudex leaves are all forked or rayed 18

18. Siliques all strongly descending, pendulous to downwardly-appressed to rachis 19

19. At least one-half of fruiting pedicels semigeniculate to geniculate at their bases 20

20. All fruiting pedicels strongly geniculate at their bases; siliques 1.0 to 1.5 mm wide; middle and upper cauline leaves revolute at edges; Alaska, Yukon, Mack. Dist., Que. (rare), Ont. (rare), Man., Sask., Alta., B.C., and southward ..... **25c.** *A. holboellii* var. *retrofracta*

20. About one-half of fruiting pedicels semigeniculate to geniculate at their bases; siliques 1.25 to 2.5 mm wide; middle and upper cauline leaves flat at edges 21

21. Siliques 1.75 to 2.5 mm broad; Greenland ..... **25a.** *A. holboellii* var. *holboellii*

21. Siliques 1.25 to 1.5 mm broad; Alaska, Yukon, Mack. Dist., Que., (rare, but common in Gaspé), Ont. (rare), Sask., Alta., B.C., and southward ..... **25d.** *A. holboellii* var. *secunda*

19. Fruiting pedicels gradually to abruptly reflexed near their bases, never semigeniculate or geniculate 22
22. Undersurfaces of caudex leaves mostly with short-stalked (less than 0.063 mm long), semidendritic to dendritic, unbranched to few-branched, 2- to 3-forked trichomes 0.25 to 0.35 mm long; these trichomes often semi-appressed to leaf surfaces and pointing towards apexes; Alaska, Yukon, Mack. Dist., Man., Sask., Alta., B.C., and southward ..... **30.** *A. pinetorum*
22. Undersurfaces of caudex leaves with sessile to medium-stalked (to 0.125 mm long), semistellate to stellate, unbranched to many-branched, 3- and 4-rayed trichomes from 0.125 to 0.35 mm wide 23
23. Middle cauline leaves weakly auriculate-, hastate- to sagittate-clasping stems; undersurfaces of caudex leaves with short-stalked (less than 0.063 mm long) semistellate trichomes, mostly 0.125 mm wide; Yukon, Sask. (Cypress Hills), sw Alta., and southward ..... **22.** *A. exilis*
23. Middle cauline leaves strongly auriculate-, hastate- to sagittate-clasping stems; undersurfaces of caudex leaves with nearly sessile stellate trichomes, mostly 0.25 to 0.35 mm wide; Sask., Alta, B.C., and southward ..... **25b.** *A. holboelli* var. *consanguinea*

18. Siliques slightly descending, spreading, strongly ascending to erect-appressed to rachis 24
24. Undersurfaces of caudex leaves mostly with medium- to long-stalked (over 0.063 mm long) rayed or forked trichomes; simple trichomes on surfaces of caudex leaves present or absent 25
25. Siliques arcuate-spreading to arcuate-descending 26
26. Undersurfaces of caudex leaves mostly with 2- and 3-forked trichomes; fruiting

plants usually have sterile rosettes with strongly ascending leaves; s B.C. (Penticton area) and southward ..... **28.** *A. sparsiflora*

26. Undersurfaces of caudex leaves mostly with 3- and 4-rayed trichomes; fruiting plants lacking sterile rosettes; Yukon, sw Alta., B.C., and southward .... **29.** *A. columbiana*

25. Siliques mostly straight and ascending, strongly ascending to erect-appressed to rachis 27

27. Cauline and caudex leaves with similar dentate to subdentate margins; flowering stems spreading to ascending 28

28. Petals less than 10 mm long and 3.5 mm wide; plants self-compatible, forming well-developed siliques; undersurfaces of caudex leaves mostly with unbranched cruciform trichomes 0.25 mm wide; Frank. Dist., Keew. Dist., Greenland, Nfld., and Que. ..... **8.** *A. alpina*

28. Petals more than 10 mm long and 3.5 mm wide; self incompatible; isolated plants with aborted siliques; undersurfaces of caudex leaves mostly with short-branched cruciform to 5-or-more-rayed trichomes; rare garden escape in Que., Ont., and B.C. ..... **9.** *A. caucasica*

27. Cauline and caudex leaves not similarly dentate to subdentate; flowering stems erect 29

29. Siliques ascending; caudex leaves with unbranched to few-branched, 2- and 3-rayed, medium-stalked (0.063 to 0.125 mm long) trichomes; siliques 1.5 to 1.75 mm wide; Yukon (rare), and B.C. (rare) ..... **20.** *A. codyi*

29. Siliques strongly ascending to erect-appressed to rachis; caudex leaves with simple to medium- (0.063 to 0.125 mm) and long- (over 0.125 mm) stalked 2- to 3-forked trichomes; siliques 1.0 to 1.75 mm wide 30

30. Biennials; petals yellow; outer sepals not saccate at bases; siliques subterete; middle and upper cauline leaves glabrous and glaucous; Alaska, Yukon, Mack. Dist., Que., Ont., Man., Sask., Alta., B.C., southward, Europe, and Asia ..... **1.** *A. glabra*

30. Biennials to short-lived perennials; petals white to purple; outer sepals saccate at bases; siliques strongly flattened; middle and upper cauline leaves pubescent, at least at bases, not glaucous 31

31. Petals small, 3 to 5 mm long; siliques 1.1 mm wide or narrower, erect-appressed to rachis; outer sepals moderately saccate at bases; cauline leaves approximate to remote 32

32. Mostly perennials; siliques beakless or nearly so; B.C. (rare); Calif., Col. and Nevada and probably more widespread south of our range; Europe ..... **6a.** *A. hirsuta* var. *hirsuta*

32. Biennials to short-lived perennials; beaks of siliques mostly 0.5 to 1.25 mm long; Alaska, Yukon, Mack. Dist., N.S., N.B., Que., Ont., Man., Sask., Alta, B.C., and southward .... **6b.** *A. hirsuta* var. *pycnocarpa*

31. Petals larger, (6) 7 to 9 (9.5) mm long; siliques 1.25 to 1.75 mm wide, somewhat divergent; outer sepals prominently saccate at bases; cauline leaves remote; Alaska and westward, Yukon, B.C. and southward ..... **7.** *A. eschscholtziana*

24. Undersurfaces of caudex leaves mostly with sessile to short-stalked (less than 0.063 mm long) rayed or forked trichomes; simple trichomes on surfaces of caudex leaves absent 33

33. Undersurfaces of caudex leaves with unbranched to few short-branched 2- to 3-rayed or forked trichomes 34

34. Siliques erect, often appressed to rachis 35
    35. Undersurfaces of rosette or caudex leaves with malpighiaceous trichomes only; Alaska, Yukon, Mack. Dist., Nfld., N.S., N.B., Que., Ont., Man., Sask., Alta., B.C., and southward ..... **14.** *A. drummondii*
    35. Undersurfaces of caudex leaves mostly with sessile 3-rayed trichomes or short-stalked 2- and 3-rayed trichomes 36
        36. Undersurfaces of caudex leaves mostly with unbranched, sessile, 3-rayed trichomes 0.25 to 0.35 mm wide; rays of trichomes appressed to leaf surfaces; bases of middle cauline leaves strongly clasping stems; sw Yukon, Mack. Dist. (rare), sw Alta., B.C., and probably southward ..... **15.** *A. calderi*
        36. Undersurfaces of caudex leaves glabrous or with mostly unbranched to few-branched, short-stalked 2- and 3-rayed trichomes 0.125 mm wide; rays and branches of trichomes elevated from leaf surfaces; bases of middle cauline leaves cuneate, truncate to very weakly auriculate; sw Yukon, s B.C., and southward ..... **21.** *A. murrayi*
34. Siliques strongly descending, descending to ascending 37
    37. Siliques to 25 mm long and 0.75 mm wide with a scattered, simple to bifurcate puberulence; petals up to 2.0 mm long; Essex Co., Ont., and southward ..... **13.** *A. shortii*
    37. Siliques more than 25 mm long and 0.75 mm wide, glabrous; petals longer than 2.0 mm 38
        38. Stems 0.7 to 2.5 (4.0) dm high; perennials with persistent, often branched, caudexes 39

39. Siliques 2.0 to 3.5 mm wide; undersurfaces of caudex leaves with sessile to short-stalked (less than 0.063 mm long) unbranched to 2-branched, 3-rayed trichomes from 0.25 to 0.35 mm wide; siliques spreading to ascending or strongly ascending; inflorescences symmetrical to secund 40
    40. Undersurfaces of caudex leaves with short-stalked, semistellate 1- to 2-branched, 3-rayed trichomes; siliques spreading to ascending; inflorescences secund; sw Yukon, sw Alta., B.C., and southward ..... **19.** *A. drepanoloba*
    40. Undersurfaces of caudex leaves with sessile to short-stalked, unbranched, 3-rayed trichomes; siliques strongly ascending; inflorescences symmetrical; sw Alta., s B.C., and southward ..... **16.** *A. lyallii*
39. Siliques 1.5 to 1.75 mm wide; undersurfaces of caudex leaves with medium-stalked (0.063 to 0.125 mm long), unbranched to few-branched, 2- and 3-forked trichomes from 0.125 to 0.25 mm long; siliques ascending; inflorescences symmetrical; sw Yukon, and nw B.C. ..... **20.** *A. codyi*

38. Stems (2) 3 to 10 dm high; biennials or short-lived perennials with compact caudexes that tend to become reduced in size as plants mature 41
    41. Undersurfaces of caudex leaves with unbranched to many prominently branched, sessile to short-stalked, 3-rayed trichomes, mostly less than 0.35 mm wide 42
        42. Undersurfaces of caudex leaves with unbranched, sessile or nearly

sessile, 3-rayed trichomes with rays appressed to leaf surfaces; inflorescences symmetrical; siliques descending, spreading to ascending; Alaska (rare), Yukon, Mack. Dist., N.B. (rare), Que., Ont., Man., Sask., Alta., B.C., and southward ..... **17a.** *A. divaricarpa* var. *divaricarpa*

42. Undersurfaces of caudex leaves with short-stalked, 3-rayed trichomes; the rays elevated above the leaf surfaces with numerous prominent branches; inflorescences semisecund to secund; siliques slightly to strongly descending; Sask., southward into U.S.A., and disjunct to Que. (rare in Gaspé) . **26.** *A. boivinii*

41. Undersurfaces of caudex leaves with unbranched to few weakly branched, short-stalked, 3-rayed trichomes, mostly more than 0.35 mm wide; se Alaska, Yukon, Mack. Dist., Que. (rare), n Ont., Man., Sask., Alta., B.C., and southward ..... **17b.** *A. divaricarpa* var. *dacotica*

33. Undersurfaces of caudex leaves with unbranched to many-branched 3- and 4-rayed trichomes 43

43. Trichomes on undersurfaces of caudex leaves mostly less than 0.25 mm wide; siliques 1.25 to 2.0 mm wide 44

44. Trichomes on undersurfaces of caudex leaves mostly between 0.125 and 0.25 mm wide; inflorescences secund; siliques mostly spreading; Yukon (rare), Alta., B.C., and southward ..... **18.** *A. lemmonii*

44. Trichomes on undersurfaces of caudex leaves mostly 0.125 mm wide; inflorescences symmetrical; siliques mostly ascending; s B.C., and southward .. .. **23.** *A. microphylla*

43. Trichomes on undersurfaces of caudex leaves mostly 0.25 or more mm wide; siliques 1.5 to 3.0 mm wide 45
45. Inflorescences secund; siliques 2.25 to 3.0 mm wide; sw Yukon, sw Alta., B.C., and southward ..... **19.** *A. drepanoloba*
45. Inflorescences symmetrical to slightly secund; siliques 1.5 to 2.0 mm wide 46
46. Siliques strongly ascending to erect; trichomes on undersurfaces of basal leaves short-stalked, semidendritic; stems 5 to 20 (40) cm high; s B.C., and southward ..... **24.** *A. depauperata*
46. Siliques spreading to descending; trichomes on undersurfaces of caudex leaves nearly sessile, semistellate to stellate; stems 30 to 60 cm high 47
47. Inflorescences symmetrical; trichomes on undersurfaces of caudex leaves mostly 0.25 mm wide; strongly perennial; frequently many stemmed; s B.C., and southward ..... **27.** *A. lignifera*
47. Inflorescences slightly secund; trichomes on undersurfaces of caudex leaves more than 0.25 mm wide; biennial or shortlived perennials; usually one to few stemmed; Sask., southward into U.S.A., and Que. (rare in Gaspé) ..... **26.** *A. boivinii*

1. **Arabis glabra** (L.) Bernh., Syst. Verg. erf. 195. 1800. Based on *Turritis glabra* L., Sp. Pl. 2: 666. 1753; Habitat in Europae, Hort. Cliff. 339. See Hopkins (1937) pp. 106 & 107 for summary of synonymy.

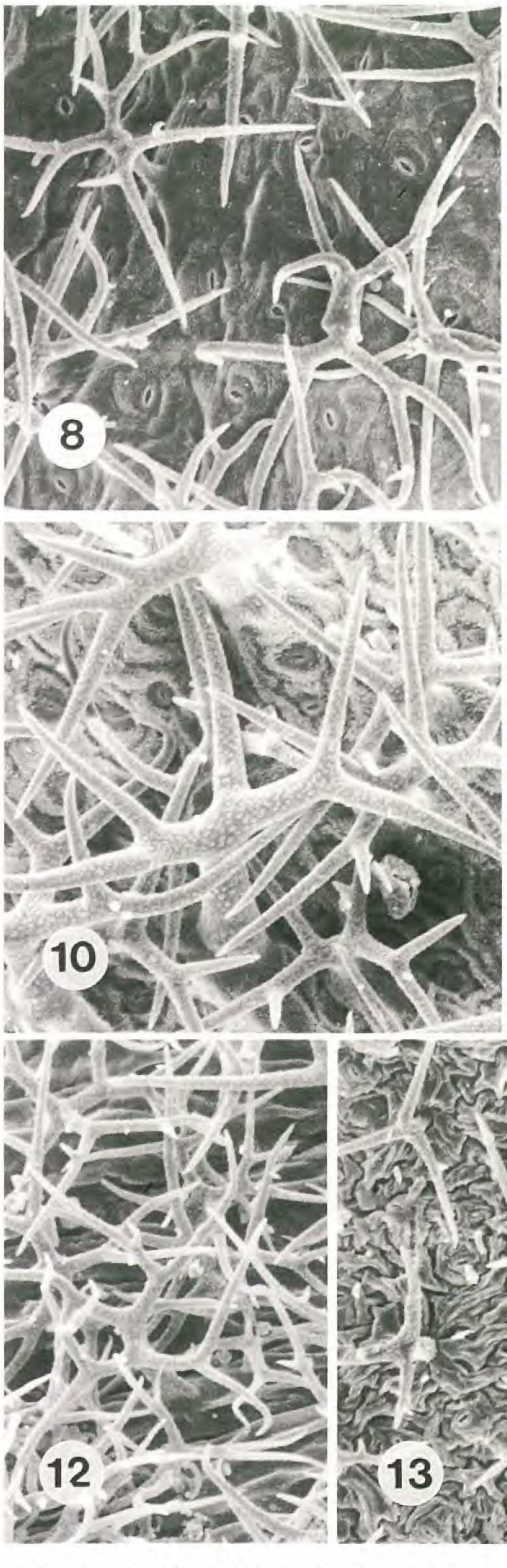
Arabis macrocarpa (Nutt.) Torr., Bot. Mex. Boundary pt. 1: 32. 1838. Based on *Turritis macrocarpa* Nutt. in T.&G., Fl. N. Am. 1: 78. 1838; Rocky situations in woods of Oregon (HOLOTYPE PH!)

Arabis glabra var. *furcatipilis* Hopkins, Rhodora 39: 109. 1937; Logan City Camp, Logan Canyon, Utah, *B. Maguire 3437* (HOLOTYPE GH!).

DISTRIBUTION. It is a native of Europe and western Asia, except in the extreme north and south, and, according to Hultén (1971) has been introduced into Africa and Australia. In North America, it is distributed widely in temperate areas of Alaska, Yukon, Quebec, Ontario, Manitoba, Saskatchewan, Alberta and British Columbia and, from Hopkins (1937), southward from Maine to North Carolina and westward to Washington, Oregon and California. It is obviously introduced at a few weedy sites in Alaska and Yukon, but occurs both in weedy and native habitats further south, particularly on sandy and sandy-loam soils of roadsides, railway embankments, open fields, riverbeds, outcrops, ledges, cliffs and openings in thickets and woods.

BIOLOGICAL NOTES. This species is sometimes removed from *Arabis* and placed in the genus *Turritis,* mostly because of its subterete siliques. I prefer to follow the treatment of Rollins (1941, p. 316) and include it in *Arabis.*

The chromosome-number $n = 6$, $2n = 12$ was obtained on North American material of *A. glabra* from Quebec, Ontario, Alberta, California, Colorado, Idaho, Montana, Oregon and Wyoming (Table 1). Pollen mother cells had 6 pairs at meiosis. Burdet (1967), combining his cytological observations and those of previous workers, reported only $2n = 12$ for plants of Canada, Austria, Bulgaria, Czechoslovakia, England, France, Germany, Hungary, Sweden and Switzerland. The $n = 8$ count of Hill (1982) on material from Virginia, therefore, needs clarification. Burdet (1967) states that the somatic chromosomes of this species are quite different from those of other *Arabis,* and uses this as a further argument that it should be placed in the genus *Turritis.* There is every indication that *A. glabra* reproduces sexually and that abundant viable seed is normally produced by selfing.



Figures 8–14. SEM photographs of *Arabis* trichomes; all ×150. Figure 8, *A. lemmonii*. Figure 9, *A. drepanoloba*. Figure 10, *A. codyi*. Figure 11, *A. murrayi*. Figure 12, *A. exilis*. Figure 13, *A. microphylla*. Figure 14, *A. depauperata*.

2. **Arabis media** N. Busch, Fl. Sib. Orient. Extrem. 1: 465. 1926; figure p. 464. *Cardaminopsis media* (N. Busch) O. E. Schulz in Engler & Prantl, Nat. Pflanzenf. 17b: 541. 1936.

Arabis media DC. var. *glabra* (DC.) Busch, Fl. Sib. Orient. Est. 4: 465. 1926. Based on part of *Arabis ambigua* DC. var. *glabra* DC., Syst. 2: 121. 1821; Unalaska.

Arabis media var. *intermedia* (DC.) Busch, Fl. Sib. Orient. Est. 4: 465. 1926. Based on part of *Arabis ambigua* DC. var. *intermedia* DC., Syst. 2: 121. 1821: Unalaska.

DISTRIBUTION. It is native to sand dunes, sand bars, tundra tussocks, disturbed gravel, river terraces and volcanic ash in arctic regions of northern Yukon, northern Alaska and adjacent northeastern Siberia. According to the distribution in the map of *Arabis arenicola* in Hultén (1968) the map should be that of *A. media.*

BIOLOGICAL NOTES. This taxon has subterete siliques, with a prominent midvein from base to apex, rather than the flattened siliques, with prominent midvein absent towards the apex, that is characteristic of most of our *Arabis* species. *Arabis media* has accumbent cotyledons. I do not consider the siliques of this species sufficiently different from our *Arabis* to warrant placing it in another genus. In fact, many workers have erroneously included specimens of *A. media* in *A. arenicola.*

Arabis media plants from two locations in Alaska had 16 somatic chromosomes (Table 1). Its basic number of $x = 8$ is the common one in Eurasiatic species of *Arabis.* It seems likely that *A. media* is a sexual species that produces seed primarily by selfing.

3a. **Arabis arenicola** (Richardson) Gelert var. **arenicola.** *Arabis arenicola* (Richardson) Gelert, Bot. Tidsk. 21: 289, 290. 1898. Based on *Eutrema arenicola* Richardson in Hooker, Fl. Bor.-Am. 1: 67. 1830; Deep sand upon shores of Arctic America, between long 107° and 150°, *Dr. Richardson* (ISOTYPE, CAN!).

Arabis humifusa (J. Vahl) S. Wats., Proc. Am. Acad. 25: 124. 1889. Based on *Sisymbrium humifusum* J. Vahl, Fl. Dan. t. 2297. 1840.

An excellent discussion of the systematics and nomenclature of *A. arenicola* var. *arenicola* and var. *pubescens* is presented on pages 77 to 80 of Hopkins (1937).

DISTRIBUTION. It is a native on sandy beaches, river banks and dunes, and on rocky shores along the north coast of Canada from the Mackenzie District to Labrador, on Southampton Island, on Baffin Island, along shores and on islands in Hudson Bay, Kenora District in northern Ontario, south shore of Lake Athabasca in northern Saskatchewan and in Greenland.

BIOLOGICAL NOTES. The chromosome number $n = 8$, $2n = 16$ has been obtained for plants of this species from Greenland and Quebec (Table 1). It has the same basic number, $x = 8$, as *A. media.* Both var. *arenicola* and var. *pubescens* are probably sexual taxa producing seed primarily by selfing.

3b. **Arabis arenicola** var. **pubescens** (S. Wats.) Gelert, Bot. Tidsk. 21: 290. 1898. Based on *A. humifusa* (J. Vahl) S. Wats. var. *pubescens* S. Wats. in Gray, Synop, Fl. N. Am. 1: 160. 1895.

DISTRIBUTION. It is native on sandy and gravel beaches and river banks along the east and west coasts of Hudson Bay and on adjacent islands in the Keewatin District, Quebec, Ontario and Manitoba, Kenora District in northern Ontario and on the south shore of Lake Athabasca in northern Saskatchewan.

4. **Arabis lyrata** L., Sp. Pl. 2: 665. 1753; Habitat in Canada, D. Kalm, Gron. virg. 76.

See Hopkins (1937), page 89 for synonomy.

DISTRIBUTION. It is native on ledges and cliffs in thickets and woods and on sandy or rocky shores of streams, rivers and lakes in the southern half of Ontario, Manitoba (rare), Saskatchewan, Alberta (localized) and in British Columbia (rare). It occurs as a rare introduction in the Mackenzie District and in Alaska. It is found in Vermont, to New Jersey and Georgia, west to Missouri, and north to Wisconsin (Rollins, 1993b).

BIOLOGICAL NOTES. *Arabis lyrata* material from two locations in Ontario had 16 somatic chromosomes (Table 1). Pollen mother cells had 8 pairs at meiosis. It is a diploid with the basic chromosome-number of $x = 8$, the same base number as *A. kamtschatica,* a tetraploid species that is frequently considered a variety or subspecies of *A. lyrata.* Other closely related taxa, are *A.*

media and *A. arenicola,* both diploids based on $x = 8$. *Arabis lyrata* is likely a sexual species producing seed by selfing.

5. **Arabis kamtschatica** (Fisch.) Ledeb., Fl. Ross. 1: 121. 1842; Kamtschatka, *ex* herb. Fisch. & labelled *Arabis kamtschatika* Fisch. (LECTOTYPE chosen LE!) *Arabis lyrata* var. *kamtschatica* Fisch. *ex* DC. Syst. 2: 231. 1821. *Arabis lyrata* subsp. *kamtschatica* (Fisch.) Hultén, Fl. Aleut. Is. 202: 1937.

Arabis kamtschatica var. *glabra* (DC.) N. Busch, Fl. Sib. Orient. Est. 4: 468. 1926. *Arabis lyrata* var. *glabra* (DC.) Hopkins, Rhodora 39: 93. 1937. Based on part of *Arabis ambigua* DC. var. *glabra* DC., Syst. 2: 121. 1821; Unalaska.

Arabis kamtschatica var. *intermedia* (DC.) N. Busch, Fl. Sib. Orient. Est. 4: 468. 1926; *Arabis lyrata* var. *intermedia* (DC.) Farwell, Mich. Acad. Sci. Rep. 256. 1917. Based on part of *Arabis ambigua* DC. var. *intermedia* DC., Syst. 2: 121. 1821; Unalaska.

Arabis occidentalis (Wats.) Nelson, Univ. Wyoming Pub. 3: 111. 1937. Based on *Arabis lyrata* var. *occidentalis* S. Wats. in Gray Syn. Fl. N. Am. 1: 159. 1895; Unalaska.

DISTRIBUTION. Moist and spring-flooded habitats in Alaska, Aleutian Islands eastern Asia, Yukon, Mackenzie District, British Columbia, Washington and south shore of Lake Athabaska in northern Saskatchewan.

BIOLOGICAL NOTES. The chromosome number $2n = 32$ has been obtained on plants growing in Alaska, Yukon and British Columbia (Table 1). It is a tetraploid with the base number of $x = 8$. It is likely a sexual species producing seed by selfing.

6a. **Arabis hirsuta** (L.) Scop. var. **hirsuta**. *Arabis hirsuta* (L.) Scop., Fl. Carn. 2: 30. 1772. Based on *Turritis hirsuta* L., Sp. Pl. 2: 666. 1753; Hort cliff. 339, habitat in Sueciae, Germaniae and Angliae.

DISTRIBUTION. Known from only one location in Canada (Mountain Creek campground and roadside, 51°26′N 117°30′W, Glacier National Park, British Columbia, elev. 2850 ft., *Haber & Shchepanek 1685,* CAN). I have seen specimens in DAO from California, Colorado and Nevada. It is probably more widespread south of Canada. It also occurs in temperate areas of Europe and Asia (Hultén, 1971).

Biological Notes. Plants from Mono Co., California and Custer Co., Colorado, had the chromosome-number $n = 16$ (Table 1). Pollen mother cells had 16 pairs at meiosis. Burdet (1967) records the chromosome-number $2n = 8$ for plants of *A. hirsuta* from one location in Switzerland and one in France, $2n = 16$ for plants from Switzerland, France, Sweden, Bulgaria and Germany and $2n = 32$ for plants from England and Norway. He suggests that $x = 4$ has to be considered as the base number for at least part of the genus *Arabis*. *Arabis hirsuta* is probably a sexual species producing seed by selfing.

6b. **Arabis hirsuta** var. **pycnocarpa** (Hopkins) Rollins, Rhodora 43: 318. 1941. Based on *Arabis pycnocarpa* Hopkins, Rhodora 39: 117. 1937; Quebec, dry ledges, St. Jean l'Evangéliste, Nouvelle Bonaventure Co., *J. F. Collins & M. L. Fernald, July 19 & 20, 1904* (Holotype GH!). *Arabis hirsuta* subsp. *pycnocarpa* (Hopkins) Hultén, Arssk. Lunds Univ. N.F. Avd. 41: 873. 1945.

Arabis rupestris Nuttall in T.&G., Fl. N. Am. 1: 81. 1838; Wahlalmet R. (Oregon), *Nuttall* (Isotype GH!).

Arabis pycnocarpa var. *reducta* Hopkins, Rhodora 39: 117. 1937; Gravelly Beach, Carlton, Tracadigash Point, Quebec, *Collins & Pease 4312* (Holotype GH!).

Arabis hirsuta var. *adpressipilis* (Hopkins) Rollins, Rhodora 43: 319. 1941. Based on *Arabis pycnocarpa* var. *adpressipilis* Hopkins, Rhodora 39: 117. 1937; Montier, Missouri, *Bush 32* (Holotype GH!).

Arabis hirsuta var. *minshallii* B. Boivin, Can. Field-Nat. 65: 16. 1951; Lemieux Island, Ottawa, Ont., *W. H. Minshall, June 26 1934* (Holotype DAO!)

Distribution. The information given by Hopkins (1937) for *A. pycnocarpa* covers my concept of *A. hirsuta* var. *pycnocarpa*: basic ledges, cliffs, bluffs, dry and rocky or moist banks and gravelly alluvium, eastern Quebec to Yukon, south to Georgia, Indiana, Illinois, Missouri, Kansas, New Mexico, Arizona and California. Workers should look for var. *hirsuta,* particularly south of the Canadian border. I have seen specimens of var. *pycnocarpa* from Alaska, Mackenzie District, Yukon, Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, Alberta and British Columbia.

Biological Notes. Plants from Mackenzie District, Manitoba, Alberta, British Columbia, Connecticut, Colorado, South Dakota and Wisconsin had the chromosome number $n = 16$, $2n$

= 32 (Table 1). Pollen mother cells had 16 pairs at meiosis. Both var. *hirsuta* and var. *pycnocarpa* plants of North America are either tetraploid based on $x = 8$ or octoploid based on $x = 4$. Burdet (1967) has suggested that the base number for *A. hirsuta* may be $x = 4$, not $x = 8$.

7. **Arabis eschscholtziana** Andrz. in Ledeb. Fl. Alt. 3: 25. 1831; *ex* insula Unalaschka, Cham. & Schtechtd. (TYPE not seen). *Arabis hirsuta* var. *eschscholtziana* (Andrz.) Rollins, Rhodora 43: 320. 1941. *Arabis hirsuta* subsp. *eschscholtziana* (Andrz.) Hultén, Arssk. Lunds Univ. N.F. Avd. 41: 872. 1945.

DISTRIBUTION. It occurs in moist habitats towards the Pacific coast in the Aleutian Islands, Alaska, Yukon, British Columbia, western Idaho, Washington and Oregon.

BIOLOGICAL NOTES. The chromosome-number $n = 32$ was obtained from plants growing in the Queen Charlotte Islands of British Columbia (Table 1). Pollen mother cells had 32 pairs at meiosis. *Arabis escholtziana* has twice the chromosome-number of North American plants of *A. hirsuta,* a species to which it is obviously closely related. They possibly also have the same basic chromosome-number, either $x = 4$ or $x = 8$. *Arabis eschscholtziana* is probably a sexual species. Although it has rather large flowers for our *Arabis* taxa, some plants growing in isolation set much seed. It is, therefore, probably a selfer.

8. **Arabis alpina** L., Sp. Pl. 2: 664. 1753; Habitat in Alpibus Helveticus, Lapponicus, Hort. cliff. 335.

Arabis incana Moench., *Arabis alpina* var. *minor* Lange, *Arabis alpina* var. *ruderalis* Wormskj., *Arabis alpina* var. *glabrata* Blytt. (see Hopkins, 1937).

DISTRIBUTION. Cliffs, ledges, rock and gravel shorelines, and alpine meadows along the west coast of Hudson Bay in Manitoba and Ontario, islands of Hudson Bay, southern shore of Baffin Island, northern shores of Quebec and Labrador, Gaspé Quebec and adjacent north shore of St. Lawrence River, Newfoundland and Greenland.

BIOLOGICAL NOTES. Plants from Greenland, Quebec and Manitoba had the chromosome number $n = 8$, $2n = 16$. Pollen mother cells had 8 pairs at meiosis (Table 1). *Arabis alpina* is probably a sexual species producing seed by selfing.

9. **Arabis caucasica** Willd., Enum. Pl. Hort. Berol. suppl. 45. 1813.

DISTRIBUTION. It is found south of the range of *A. alpina* in Europe and Asia (Hultén, 1958). It persists as a rare garden escape in Quebec, Ontario and British Columbia.

BIOLOGICAL NOTES. Plants growing as a garden escape in Ontario had 8 pairs of chromosomes at meiosis (Table 1). Since isolated plants produce little or no seed, it is likely that *A. caucasica* is a sexual outcrosser. It is closely related to *A. alpina* and is considered a variety or subspecies of *A. alpina* by some workers.

10. **Arabis nuttallii** Robinson in Gray, Syn. Fl. N. Am. 1: 160. 1895; R. Mts, *Nuttall* (HOLOTYPE PH!; ISOTYPE GH!).

Arabis bridgeri M. E. Jones, Contrib. West. Bot. 14: 38. 1912; Mt. Bridger, Gallatin Co., Montana, *M. E. Jones, Aug. 10, 1905* (HOLOTYPE PH, not seen).
Arabis macella Piper, Proc. Biol. Soc. Wash. 33: 103. 1920. Ritzville, Adams Co., Washington, *Sandberg & Leiberg 202* (HOLOTYPE US, not seen).

DISTRIBUTION. Grassy slopes and benches, prairie hillsides, open thickets and woods, and roadsides in Yukon (very rare), southwest Alberta, southeast British Columbia, Montana, Wyoming, Utah, Idaho, Washington and Nevada.

BIOLOGICAL NOTES. I have seen no information on the chromosome number of *A. nuttallii.* Since isolated plants have some aborted siliques and plants growing in dense colonies have all well-formed siliques, it is possible that this relatively large flowered *Arabis* is a sexual outcrosser.

11. **Arabis canadensis** L., Sp. Pl. 2: 665. 1753; *Eruca virginiana* Pluk. alm. 136.

Arabis falcata Michx., Fl. Bor. Am. 1: 31. 1803 and *Arabis mollis* Rafinesque, Am. Month. Mag. 2: 43. 1817 *non* Steven, Bull. Soc. Nat. Mosc. 2: 270. 1812 (see Hopkins, 1937, p. 178).

DISTRIBUTION. Rich woods, thickets and rocky banks, southwestern Quebec, southern Ontario. It also occurs from Maine to Florida, and westward to Texas, Nebraska and Minnesota (Rollins, 1993b).

BIOLOGICAL NOTES. The chromosome-number of $2n = 14$ has been reported for plants growing in southern Ontario (Table 1). It has the basic number, $x = 7$, that is very common for North American species of *Arabis.*

12. **Arabis laevigata** (Mühl.) Poir., Encyl. Suppl. 1: 411. 1810. Based on *Turritis laevigata* Mühl., Index Fl. Lancastr. in Trans. Am. Phil. Soc. 3: 1793.

Arabis lyraefolia DC., Syst. 2: 244. 1821; *Arabis heterophylla* Nutt. *ex* T.&G., Fl. N. Am. 1: 81. 1838; *Arabis hastata* Eaton, Man. Bot. ed. 2: 141. 1818 (all after Hopkins, 1937).

Arabis missouriensis Greene, in Feddes Repertorium 5: 244. 1908; Montier, Missouri, *B. F. Bush 31* (HOLOTYPE ND!).

DISTRIBUTION. Rich rocky woods, rocky hillsides and ledges, southwestern Quebec, southern Ontario. It is also found from New Jersey to Georgia, west to Oklahoma and Kansas, and north to Minnesota (Rollins, 1993b).

BIOLOGICAL NOTES. The chromosome-number $n = 7$ was obtained for plants from Connecticut, Maryland and Wisconsin (Table 1). Pollen mother cells had 7 pairs of chromosomes at meiosis. *Arabis laevigata* is probably a sexual species producing seed by selfing.

13. **Arabis shortii** (Fern.) Gleason, Phytologia 4: 23. 1952; *Arabis perstellata* E. L. Braun var. *shortii* Fernald, Rhodora 48: 208. 1946. Based on *Sisymbrium dentatum* Torrey in Short, 3rd Suppl. Cat. Pl. Kentucky, 338. 1833; On the sandy banks of the Ohio river, Fl. April, *C. W. Short* (LECTOTYPE DWC!).

Arabis shortii (Fern.) Gleason var. *phalacrocarpa* (Hopkins) Steyerm., Rhodora 62: 130. 1960. Based on *Arabis dentata* var. *phalacrocarpa* Hopkins, Rhodora 39: 169. 1937; Along shaded limestone bluffs of Osage River, near Osceola, St. Clair County, Missouri, *E. J. Palmer 35650* (HOLOTYPE GH!).

DISTRIBUTION. Shady banks and bottomlands and on limestone bluffs and ledges in rich woods, Essex County in Ontario. It also occurs from New York to Virginia, Tennessee and Alabama, west to Kansas, and Nebraska, and north to Minnesota (Rollins, 1993b).

BIOLOGICAL NOTES. The chromosome number of $n = 7$ reported for *Arabis perstellata* (Table 1), probably does not apply to *A. shortii*. The holotype of *A. perstellata* in GH has cauline leaves cuneate at bases not sagittate-clasping as in *A. shortii*.

14. **Arabis drummondii** Gray, Proc. Am. Acad. 6: 187. 1863. Based on *Turritis stricta* Graham, Edinburg New Phil. Jour. 350, 1879; plant grown from seeds collected by Drummond in Rocky Mts. (see Hopkins, 1937, p. 146).

Arabis albertina Greene, in Pittonia 4: 196. 1900; Alberta, Elbow River, Rocky Mountains, *J. Macoun 18101* (HOLOTYPE ND!).

Arabis drummondii var. *oxyphylla* (Greene) Hopkins, Rhodora 39: 143. 1937. Based on *Arabis oxyphylla* Greene, in Pittonia 4: 197. 1900; Near Pagosa Peak, Colorado, *C. F. Baker 747* (HOLOTYPE ND!).

Arabis drummondii var. *connexa* (Greene) Fernald, Rhodora 5: 231. 1903. Based on *Arabis connexa* Greene, in Pittonia 4: 197. 1900; Near Pagosa Peak, Colorado, *C. F. Baker 341* (HOLOTYPE & 3 ISOTYPES ND!).

DISTRIBUTION. Open, often calcareous, habitats in Alaska, Yukon, Mackenzie District, Newfoundland, Labrador, Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, Alberta and British Columbia. It is widespread from New Jersey, west to northern Arizona and the Sierra Nevada of California, and north to Washington (Rollins, 1993b).

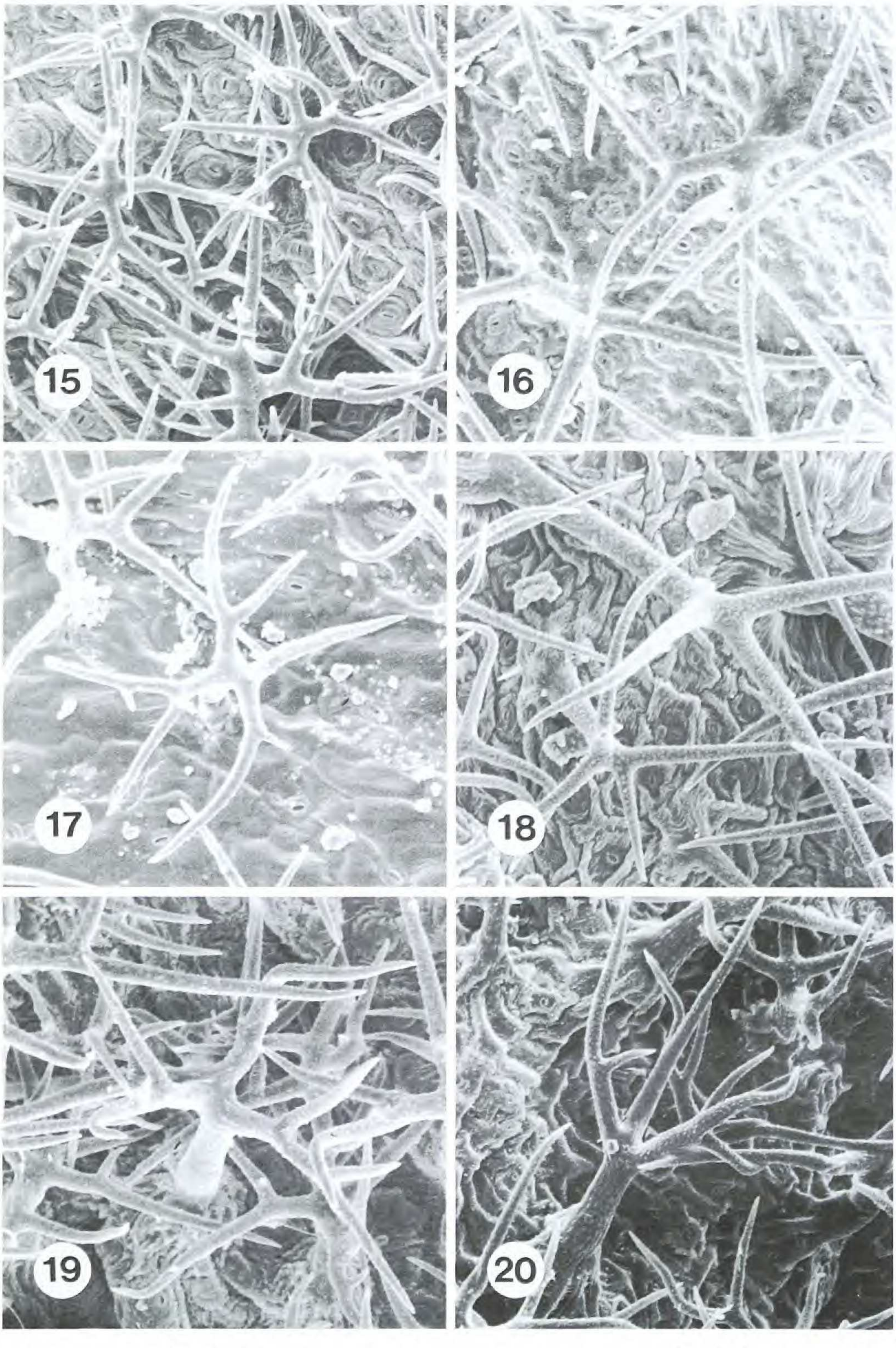
BIOLOGICAL NOTES. *Arabis drummondii* is one of our most widespread species. Siliques tend to be narrower and the basal or caudex leaves glabrous or nearly so in the eastern part of its range. This species seems to be most closely related to *A. calderi* and through *A. lyallii* to *A. divaricarpa*. *Arabis drummondii* contains diploid, triploid and tetraploid chromosome races based on $x = 7$ (Table 1). Most diploids from Yukon, Alberta, California, Colorado, Montana, Utah and Wyoming had 7 pairs at meiosis. These plants were probably sexual, producing seed by selfing. The triploids from Alberta and British Columbia almost certainly produce seed by apomixis. According to Böcher (1969) the tetraploid plants from Massachusetts were probably sexual as their pollen had the reduced number of 14.

15. **Arabis calderi** G. Mulligan, *sp. nov.*

Arabis calderi ab A. drummondia 3-radiatis trichomatibus et siliquis angustioribus differt et ab A. lyallii et ab A. divaricarpa siliquis erectis et rachidi adpressis differt.

Arabis calderii differs from *Arabis drummondii* by its 3-rayed trichomes and narrower siliques and from *Arabis lyallii* and *Arabis dicaricarpa* by its siliques being erect and appressed to the rachis.

The holotype specimen, in the herbarium of Agriculture Canada, Ottawa (DAO), is named after James Alexander Calder, 1915–1990 (*see* tribute to Calder by Cody & Cayouette, 1991). British Columbia, Indian River at Mile 34 from Alaska Highway on Atlin Road, approx. 59°54′N, 133°48′W, common on open grassy flats



Figures 15–20. SEM photographs of *Arabis* trichomes; all ×150. Figure 15, *A. holboelli* var. *retrofracta*. Figure 16, *A. boivinii*. Figure 17, *A. lignifera*. Figure 18, *A. sparsiflora*. Figure 19, *A. columbiana*. Figure 20, *A. pinetorum*.

on bench above river, *J. A. Calder & J. M. Gillett 25180,* June 9, 1960 (HOLOTYPE DAO!).

Perennial with a simple or branched caudex; stems erect, one to several, simple to once-branched, 7.5 to 40.0 cm high; cauline leaves entire, glabrous, sessile, mostly strongly sagittate-clasping stems, narrowly lanceolate, 1 to 4 cm long, 1 to 4 mm wide; caudex leaves entire, numerous and rosulate, 1 to 3 cm long, 2 to 6 mm wide, the blades narrowly oblanceolate, slender petiolate; lower surfaces of caudex leaves with sparse to scattered sessile, unbranched 3-rayed trichomes 0.25 to 0.35 mm wide; inflorescences symmetrical, usually congested; sepals purplish, oblong to narrowly oblong, saccate at bases, 3 to 4 mm long, 0.75 to 1.0 mm wide; petals purplish, narrowly cuneate, 7.0 to 7.5 mm long, 0.75 to 1.5 to 1.75 mm wide; style rudimentary; seeds mostly in 2 rows, brownish, oval, 1.75 mm long, 1.25 mm wide, prominently winged on sides and apex, cotyledons accumbent.

DISTRIBUTION. Grassy clearings, meadows and openings in thickets in subalpine and alpine areas of southwestern Yukon, Great Bear Lake of Mackenzie District, southwest corner of Alberta and in British Columbia. It is probably commoner than the number of herbarium collections indicate. No specimens were seen from the adjacent United States, but it almost certainly occurs there.

BIOLOGICAL NOTES. It is most closely related to *A. drummondii* and *A. lyallii.* All of the specimens of *A. calderi* seen in herbaria were previously identified mostly as *A. drummondii* and occasionally as *A. lyallii* or *A. divaricarpa.* Although no chromosome numbers have been determined from plants of *A. calderi,* I would predict a base number of $x = 7$.

REPRESENTATIVE SPECIMENS. CANADA. **Yukon:** Vicinity of Mackintosh (mile 1022, Alaska Highway), roadside, flowers purplish tinged, slightly glaucous, *Schofield & Crum 7348* (CAN, UBC); Vicinity of Pine Creek, Alaska Highway near mi. 1019, app. 60°47′N, 137°35′W, prairie, *Raup et al. 13033* (ALA, CAN, UBC); Canol Rd., Mile 132, Lower Lapie R. Crossing, slopes near timberline, 5000′, *Porsild & Breitung 9722* (CAN); Mile 25 from Alaska Highway on road to Dawson, 61°08′N, 135°20′W, occasional in openings in dwarf birch-willow thickets on flats at 2600′, flowers dark mauve, *Calder & Gillett 25788* (ALA, DAO); Champagne at Mile 974, Alaska Highway, 60°47′N, 136°29′W, in slightly saline grassy clearing between spruce-Aspen . . . , flowers mauve,

alt. 2300′, *Calder & Gillett 25142* (DAO). **Mackenzie District:** Great Bear Lake, north shore of Smith ARM, Olmstead Bay, about 66°32′N, 122°35′W, calcareous soil *Porsild & Porsild 5080* (CAN); Great Bear Lake, Etacho Point (Big Point), elevation about 1500 feet, 66°N, 121°30′W, *Porsild & Porsild 3494B,* sheet is mixture of 2 plants of *A. calderi* and 1 plant of *A. drummondii* (CAN). **Alberta:** Lake Agnes above Lake Louise, Banff National Park, occasional on dry, gravelly-rocky slopes at treeline, alt. 7000′, *Calder 24021* (DAO); Crandell Trail and Akamena Hwy., 49°05′N, 113°58′W, partly exposed on steep SE hill, 5200′, Waterton Lakes National Park, *Blais 1996* (CAN). **British Columbia:** Blustry Mountain, 50°36′N, 121°42′W, 2256 m, *Johns 584* (DAO, UBC); old Jackson Mine Road, south of New Denver-Kaslo Road, 50°01′N, 117°09′W, ca. 6000′, *Beamish et al. 750328* (DAO, UBC); Cornwall Mtn., Lookout Rd., southwest of Ashcroft, ca. 6000 ft., *Beamish 630166* (DAO); Cairn Peak, Upper Hat Creek, 7600 ft., *Brink 49-514* (UBC).

16. **Arabis lyallii** S. Watson, Proc. Am. Acad. 11: 122. 1875. Based on *Arabis drummondii* var. *alpina* S. Watson in King, Geol. Expl. Fortieth Parallel 5: 18. 1871; Clover Mts., N. Nevada, 10,000 ft. alt., *S. Watson 75* (HOLOTYPE GH!).

Arabis oreophila Rydb., Bull. Torr. Bot. Club 3: 437. 1907; Divide between Big Cottonwood Canyon and Heber Valley, *P. A. Rydberg & E. C. Carlton 6678* (HOLOTYPE NY!).

Arabis amerifolia Greene, Leaflets Bot. Obs. Crit. 2: 75. 1910; On a firm pumice slope, Crater Lake National Park, Oregon, *F. V. Coville 1504* (HOLOTYPE US!)

Arabis multiceps Greene, Leaflets Bot. Obs. Crit. 2: 76. 1910; On open rocky slope, Mount Thielson, Cascade Mts., Oregon, *F. V. Coville & E. I. Applegate 435* (HOLOTYPE US!).

Arabis densa Greene, Leaflets Bot. Obs., Crit. 2: 76. 1910; Eagle Cap, Imnaha National Forest, Oregon, 9500 feet, *A. W. Sampson & G. A. Pearson 206* (HOLOTYPE US!).

Arabis davidsonii Greene, Leaflets Bot. Obs. Crit. 2: 159. 1911; Bishop Creek, Inyo Co., Cal., *A. Davidson 2728* (LECTOTYPE RSA!). *Arabis lyallii* var. *davidsonii* (Greene) Smiley, Univ. Calif. Pub. Bot. 9: 205. 1921.

DISTRIBUTION. Occurs in alpine and subalpine areas in shale and rock crevices and in meadows in southwestern Alberta and southern British Columbia. It also occurs southward into Montana, Idaho, Washington, Wyoming, Utah, Nevada, Oregon and California (Rollins, 1941).

BIOLOGICAL NOTES. *Arabis lyallii* seems to be the alpine and subalpine phase of the more widespread *A. divaricarpa.* It also resembles the latter species in that some plants have glabrous caudex leaves. *Arabis lyallii,* at least in our range, is more uniform morphologically than *A. divaricarpa.* Plants of *Arabis lyallii* from Alberta and Utah were triploid, based on $x = 7$. These must therefore produce seed by apomixis.

17a. **Arabis divaricarpa** A. Nelson var. **divaricarpa.** *Arabis divaricarpa* A. Nelson, Bot. Gaz. 30: 193. 1900; Yellowstone Lake, on the stony and sandy banks of the lake, Yellowstone National Park, *A. & E. Nelson 6622* (LECTOTYPE chosen by Hopkins, 1937, RM!; ISOLECTOTYPE GH!).

Arabis brachycarpa (T.&G.) Britton, Mem. Torre. Bot. Club. 5: 174. 1894. *Non* Ruprecht, Fl. Cauc. 73. 1869. Based on *Turritis brachycarpa* T.&G., Fl. N. Am. 1: 79. 1838; Fort Gratiot, Michigan and shore of Lake Superior, *Dr. Pitcher* (HOLOTYPE NY!).

Arabis nemophila Greene, Leaflets Bot. Obs. & Crit. 2: 78. 1910; Sequoia National Forest, California, *A. Davidson 1847* (HOLOTYPE US!).

Arabis brevisiliqua Rydberg, Bull. Torr. Bot. Club 39: 326. 1912; Skagit Valley, B.C., *J. M. Macoun 70825* (HOLOTYPE NY!; ISOTYPE CAN!).

Arabis drummondii var. *pratincola* (Greene) Hopkins, Rhodora 39: 142. 1937. Based on *Arabis pratincola* Greene, in Feddes Repertorum 5: 244. 1908; Spooner, Douglas County, Nevada, *C. F. Baker 1149* (ISOTYPES GH!, MO!).

Arabis patula (Graham) Torrey var. *stenocarpa* (Hopkins) Farwell, Papers Mich. Acad. Sci. 26: 14. 1941. Based on *Arabis divaricarpa* var. *stenocarpa* Hopkins, Rhodora 39: 133. 1937; Quebec, slaty ridges east of Bic, Rimouski Co., *M. L. Fernald & J. F. Collins 1057* (HOLOTYPE GH!; ISOTYPE CAN!).

DISTRIBUTION. Open disturbed areas on cliffs and rock outcrops, in woods on shorelines and along roadsides in Alaska (rare), southern Yukon, Mackenzie District, New Brunswick (rare), Quebec, Ontario, Manitoba, Saskatchewan, Alberta, British Columbia and southward into the United States, particularly in the east.

17b. **Arabis divaricarpa** var. **dacotica** (Greene) B. Boivin, Am. Midl. Nat. 54: 510. 1955. Based on *Arabis dacotica* Greene, Leaflets Bot. Obs. & Crit. 2: 80. 1910; Fort Meade, South Dakota, *W. H. Forwood 28* (HOLOTYPE US!).

Arabis oblanceolata Rydb., Bull. Torr. Bot. Club 31: 557, 1904, Valley Spur, Colorado, *L. M. Underwood & A. D. Selby 454* (HOLOTYPE NY!).

Arabis divaricarpa var. *hemicylindrica* B. Boivin, Am. Midl. Nat. 54: 510. 1955; Maple Creek, Sask., 10 milles au sud Carmichael, monts Cyprès, écorre de

la coulée du ruisseau Bone, *B. Boivin & J. Alex 9738* (HOLOTYPE DAO!). A specimen with the identical label data, in SASK, is *Arabis pinetorum.*

DISTRIBUTION. Open, dry, often sandy, disturbed areas of prairie, grasslands, hillsides and shorelines in southeast Alaska, central and southern Yukon, Mackenzie District, Quebec (rare, Co. Témiscamingue), northern Ontario, Manitoba, Saskatchewan, Alberta, British Columbia and southward into the United States, particularly from Minnesota westward.

BIOLOGICAL NOTES. It is morphologically the most variable of our *Arabis* species. The siliques range from ascending to descending, surfaces of rosette or caudex leaves may be glabrous to densely covered with sessile to short-stalked 3-rayed trichomes. The 3-rayed trichomes are from less than 0.25 mm in diameter to more than twice that wide and rays are appressed to leaf surfaces to divergent. It is often difficult to distinguish some western plants of *A. divaricarpa* from *Arabis lyallii,* particularly fragmentary material. However, complete and mature plants of *A. lyallii,* a more montane plant, can be reliably separated from *A. divaricarpa.* Although there is some morphological overlap between var. *divaricarpa* and var. *dacotica,* they seem to have slightly different habitats and distributions. Plants of var. *divaricarpa* from Saskatchewan, Alberta, British Columbia, Montana and California were diploid or tetraploid, based on $x = 7$, whereas plants of var. *dacotica* from the Mackenzie District, Manitoba, British Columbia and Colorado were diploid, triploid or tetraploid, with the same base number (Table 1). One of the diploids formed 7 pairs of chromosomes at meiosis. Böcher (1969) reported that EMCs, PMCs and pollen grains of *A. divaricarpa* plants from California had the aneuploid number of $2n = 22$ and dyads and uniform pollen grains were formed. Mosquin (Table 1) found that tetraploid plants from Manitoba had an irregular meiosis. In addition, some plants have supplementary chromosomes ($2n = 13 + 2B$). It, therefore, appears that *A. divaricarpa* has diploids, triploids and tetraploids, that some of the diploids are probably sexual selfers, that triploids are apomictic, and that at least some of the tetraploids are also apomictic. The reproductive system of *A. divaricarpa* is obviously very complex. Rollins (1983) suggested that *A. divaricarpa* can either: **a.** be considered a natural hybrid taxon that includes stable populations of ancient hybrid origin, less stable more recently produced hybrids, and many hybrid populations produced under intermediate conditions; or **b.** be

considered a polytypic species of ancient hybrid origin. I have observed no morphological evidence of any recent interspecific hybridization in our *Arabis* species.

18. **Arabis lemmonii** S. Watson, Proc. Am. Acad. 22: 467. 1887; Lassen's Peak, *Lemmon 23* (LECTOTYPE GH!).

Arabis latifolia (S. Wats.) Piper, Contrib. U.S. Nat. Herb. 295. 1906. Based on *Arabis canescens* Nutt. var. *latifolia* Watson in King, Geol. Expl. Fortieth Parallel 5: 17. 1871; Clover Mts., Nevada, 11,000 ft., *S. Watson* 71 (HOLOTYPE GH!).

Arabis kennedyi Greene, Leaflets Bot. Obs. & Crit. 2: 71. 1910; Galena Creek, Washoe Co., Nevada, *P. B. Kennedy 1248* (HOLOTYPE US!; ISOTYPE NY!).

Arabis oreocallis Greene, Leaflets Bot. Obs. & Crit. 2: 73. 1910; Beaverfoot Mts., Selkirk & Rky. Mts., British Columbia, *C. H. Shaw 315* (HOLOTYPS US!).

Arabis semisepulta Greene, Leaflets Bot. Obs. & Crit. 2: 74. 1910; Near summit in loose lava gravel, Mount Thielson, Cascade Mountains, Oregon, *F. V. Coville & E. I. Applegate 454* (HOLOTYPE US!; ISOTYPE RM!).

Arabis polyclada Greene, Leaflets Bot. Obs. & Crit. 2: 75. 1910; Farwell Gap, California, *C. A. Purpus 5229* (HOLOTYPE US!; ISOTYPES GH!, UC!).

Arabis egglestonii Rydb., Fl. Rocky Mts., 316. 1918; Clover Mountain, above Garfield, Colorado, *W. W. Eggleston 6013* (HOLOTYPE NY!).

DISTRIBUTION. Rock and gravel alpine slopes in Yukon (rare, Mt. Archibald), southwestern Alberta and southern British Columbia. Occurs southward in Montana, Idaho, Washington, Wyoming, Colorado, Utah, Nevada, Oregon and California (Rollins, 1941).

BIOLOGICAL NOTES. *Arabis lemmonii* plants from Alberta, British Columbia and Wyoming were reported to be diploid, based on $x = 7$, and from Montana were found to be triploid, with the same base number. The latter plants, producing large amounts of seed, were obviously apomictic.

19. **Arabis drepanoloba** Greene, Pittonia 3: 306. 1898; Devil's Head Lake, Banff National Park, Alberta, *Macoun 1719a* (HOLOTYPE ND!; ISOTYPE US!).

DISTRIBUTION. Alpine meadows and ridges in Colorado, Wyoming, Montana, southwest Alberta, southeast British Columbia and disjunct to southwest Yukon.

BIOLOGICAL NOTES. Although there are no chromosome counts for this species, I suspect that it belongs to *Arabis* species with the base number $x = 7$. It is most similar to *A. lemmonii* but I

think that the two entities should be treated as separate species because of the much larger trichomes and siliques in *A. drepanoloba*.

20. **Arabis codyi** G. Mulligan, *sp. nov.*

Arabis codyi ab A. drepanoloba et ab A. lyallii differt siliquis angustioribus 1.5–1.75 mm latis et trichomatibus furcatis potius quam radiatis.

Arabis codyi differs from *A. drepanoloba* and *A. lyallii* by its narrower, 1.5 to 1.75 mm wide, siliques and forked, rather than rayed trichomes.

The holotype specimen in the herbarium of Agriculture Canada, Ottawa, is named after William James Cody (1922–). Yukon, Kaskawulsh nunatak, jct. N and central arms Kaskawulsh Glacier, W of Kluane Lake, 6000 ft., unstable slopes, *D. F. & D. B. Murray 72*, 1 July–1 August, 1965 (HOLOTYPE DAO!).

Perennial with a simple or branched caudex; stems erect to ascending, one to several, simple, 7 to 14 cm high; cauline leaves entire, rarely few toothed, glabrous or with scattered short-stalked, unbranched to few branched, 2- and 3-forked trichomes from 0.125 to 0.25 mm long, leaves sessile, mostly sagittate clasping stems, narrowly lanceolate to lanceolate, 0.5 to 1.5 cm long, 1.5 to 3.0 mm wide; caudex leaves entire to rarely with 1 to 2 shallow lobes towards apex, numerous and rosulate, 0.75 to 1.5 cm long, 1.5 to 3.0 mm wide, the blades narrowly oblanceolate to oblanceolate, slender petiolate; lower surfaces of caudex leaves densely pubescent with short stalked, unbranched to few-branched, 2- and 3-forked trichomes from 0.125 to 0.25 mm long; inflorescences symmetrical, open; sepals purplish, oblong, saccate at bases, 2.5 to 3.0 mm long, 1.5 to 1.75 mm wide; petals purplish, cuneate, 6.5 mm long, 2.0 mm wide; fruiting pedicels ascending, straight, 3 to 5 mm long; siliques ascending, straight to slightly curved, 2.0 to 3.75 cm long, 1.5 to 1.75 mm wide, abruptly tapering at apex to a rudimentary style.

The only other specimen seen was collected in British Columbia: Perow, B.C., 54°30′N, 126°26′W, growing on sandy beach, 700 m, *Taylor & Levis 468* (UBC).

21. **Arabis murrayi** G. Mulligan, *sp. nov.*

Arabis murrayi a ceteris Arabibibus praeditis foliis mediis caulinis basi cuneatis vel raro infirme auriculatis, siliquis erectis rachidi adpressis differt. A. murrayi

plerumque A. lyallii confusa est, specie praedita foliis caulinis valde sagittao-amplexicaulibus.

Arabis murrayi differs from other *Arabis* that have the bases of middle cauline leaves cuneate to rarely weakly auriculate, by its erect siliques which are appressed to the rachis. It is usually misidentified as *A. lyalli,* a species with strongly sagittate-clasping cauline leaves.

The holotype specimen in the herbarium of Agriculture Canada, Ottawa, is named after David F. Murray, University of Alaska, College. Yukon, Kaskawulsh nunatak, jct. N. and central arms Kaskawulsh Glacier, W of Kluane Lake, 6000 ft., *D. F. & B. M. Murray 91b,* 1 July–1 August, 1965 (HOLOTYPE DAO!; ISOTYPE ALA!).

Perennial with a simple or branched caudex; stems erect, one to several, simple, 2.5 to 15.0 cm high; cauline leaves entire, glabrous or with scattered short-stalked, unbranched to few branched 2- and 3-rayed trichomes mostly 0.125 mm wide, leaves sessile, cuneate to rarely weakly auriculate at bases, lanceolate, 0.3 to 1.0 cm long, 1 to 3 mm wide; caudex leaves numerous and stiffly ascending, 0.5 to 1.75 cm long, 0.75 to 1.5 mm wide, the blades narrowly oblanceolate, slender petiolate; lower surfaces of caudex leaves with scattered to dense short-stalked, unbranched to few branches, 2- and 3-rayed trichomes mostly 0.125 mm wide; inflorescences symmetrical, short, few-fruited, congested; sepals slightly purplish, oblong to narrowly oblong, nonsaccate at bases, 3 mm long, 1 mm wide; petals whitish, linear-oblong, 6.5 mm, 0.5 mm wide; fruiting pedicels erect, straight to slightly curved, 3 to 4 mm long; siliques erect, appressed to rachis, straight, 2.0 to 4.5 cm long, 1.5 to 2 mm wide, style *ca.* 0.125 mm long; seeds oval, in 2 rows, brownish, 1.0 mm long, 0.75 mm wide, prominently winged only at apex, cotyledons accumbent.

DISTRIBUTION. Alpine slopes in southwestern Alberta, southern British Columbia, Washington and probably Idaho and western Montana. It apparently has a disjunct distribution to the southwestern corner of Yukon.

BIOLOGICAL NOTES. Nearly all of the *A. murrayi* material that I have examined in herbaria were misidentified as *A. lyallii* and many sheets were mixtures of the two taxa. *Arabis murrayi* has cauline leaves that are cuneate to rarely weakly auriculate; trichomes on undersurfaces of caudex leaves, if present, are un-

branched to few branched, 2- and 3-rayed, and mostly 0.125 mm wide; and siliques are erect and appressed to the rachis. *Arabis lyallii* has cauline leaves that are strongly sagittate-clasping the stems, trichomes on undersurfaces of caudex leaves, if present, are unbranched, 3-rayed, and mostly 0.25 mm wide; and siliques are strongly ascending. The surfaces of the caudex leaves of both species are often glabrous.

REPRESENTATIVE SPECIMENS. CANADA. **Yukon:** Kaskawush nunatak, jct. N. and central arms Kaskawush Glacier, W. of Kluane Lake, unstable slopes, 6000 ft., *Murray & Murray 41A,* also contains plants of *A. drepanoloba* labelled *41B* (ALA, CAN). **Alberta:** Crypt Lake, Waterton Park, open slope, 6600′, *Scotter 9881B,* also contains plants of *A. lyallii* labelled *9881A* (DAO). **British Columbia:** Akamina Ridge on B.C.-Alberta border, 49°01′N, 114°04′W–114°07′W, occasional on rocky shade exposed summit ridge between 8000′ & 8400′, *Taylor et al. 3547* (DAO); Cathedral Lakes, Ashnola Dist., 49°N, 120°15W, rock slide on shoulder of Pyramid Mt., 7000′, cor. purple, *Taylor 1370* (UBC); Finlayson Peak overlooking Maselpanik Creek, 7200 feet, purple flowers, *Pinder-Moss & Hamlyn 1157* (UBC); Blackwell Peak, north of ranger station along Hope-Princeton Highway, occasional on rocky, east-facing slope, alt. 6300′, flowers purplish-blue; *Calder & Saville 10551A,* also contains plants of *A. lyallii* labelled *10551B* (DAO). UNITED STATES. **Washington:** Yakima Co., alpine slopes of Mt. Aix, Snoqualmie Nat. Forest, 7000 feet, *Thompson 15045a* (DAO); Chelan Co., ridge ½ mi. W of Hoodo Pass and ca. 16 mi. SSW of Twisp, in dry herbfield, alpine zone, aspect S20W, slope 20%, 6830′, *Douglas & Douglas 4143* (DAO).

22. **Arabis exilis** A. Nelson, Bull. Torrey Bot. Club. 26: 123. 1899; Evanston, Wyoming, *A. Nelson 4523* (LECTOTYPE RM!, centre specimen (A) best fits description of *A. exilis,* outer two specimens (B) are *Arabis holboellii* var. *retrofracta*; ISOLECTOTYPE GH!).

Arabis pendulocarpa A. Nelson, Bot. Gaz. 30: 192. 1900; On cliffs and rocky ridges, Madison River, Yellowstone National Park, *A. & E. Nelson 5504* (LECTOTYPE RM! by Rollins 1941; ISOLECTOTYPES GH!, NY!, RM!, US!). *Arabis holboellii* var. *pendulocarpa* (A. Nels.) Rollins, Rhodora 43: 446. 1941.

DISTRIBUTION. On rocky and grassy subalpine slopes and prai-

rie in southcentral Yukon, Cypress Hills Saskatchewan, Cypress Hills Alberta, southwest Alberta and British Columbia. Herbarium specimens were also seen from Montana, Washington, Utah, Colorado and Nevada. It undoubtedly occurs elsewhere in the western United States.

BIOLOGICAL NOTES. Plants from Yukon, British Columbia and Montana were diploid, based on $x = 7$, whereas those from Utah were triploid (Table 1). One of the diploids from British Columbia formed 7 pairs of chromosomes at meiosis (Taylor and Taylor, 1977). This species probably contains sexual and apomictic plants. Böcher (1969, p. 146) grew material of this species in experimental plots alongside plants of *A. holboellii* and concluded that it should no longer be included in the *A. holboellii* complex.

23. **Arabis microphylla** Nuttall in T.&G., Fl. N. Am. 1: 82. 1838; Rocky Mountains, *Nuttall* (HOLOTYPE PH!).

Arabis macounii Watson, Proc. Am. Acad. 26: 124. 1891; Gravelly banks, Eagle Pass, W of Revelstoke B.C., *J. Macoun, May 13th, 1890* (HOLOTYPE GH!; ISOTYPES CAN!, MO!, PH!, US!). *Arabis microphylla* var. *macounii* (Watson) Rollins, Rhodora 43: 428. 1941.

Arabis paupercula Greene, Leaflets Bot. Obs. & Crit. 2: 77. 1910; Farwell Gap, southeastern California, 10,600, *C. A. Purpus 5229½* (HOLOTYPE US!; ISOTYPES MO!, UC!).

Arabis tenuicula Greene, Leaflets Bot. Obs. & Crit. 2: 82. 1910; Crevices of cliffs, Union Co., Oregon, *W. C. Cusick 1124* (HOLOTYPE US!; ISOTYPE GH!).

Arabis microphylla var. *saximontana* Rollins, Rhodora 43: 429. 1941; Granitic hillsides, Porcupine Creek, near Medicine Mountain, Big Horn County, Wyoming, alt. 8500 ft., *L. O. & R. Williams 3264* (HOLOTYPE GH!).

Arabis lemmonii var. *paddoensis* Rollins, Rhodora 43: 384. 1941; Rocks, Mount Paddo, Washington, 6 or 7000 ft. alt., *W. N. Suksdorf 509* (HOLOTYPE GH!).

DISTRIBUTION. In crevices on rock cliffs and large boulders in southcentral British Columbia and, according to Rollins (1941), from Montana and Wyoming to Nevada and Washington.

BIOLOGICAL NOTES. This species has the chromosome number $n = 7$ and 15/2 and $2n = 14$ and 15 (Table 1). Böcher (1969) stated that plants from Wyoming had PMCs forming dyads, and anaphases initiating dyads were all regular with 15 chromosomes. *Arabis microphylla* obviously contains apomictic diploid plants with the base number $x = 7$, some of which have an aneuploid number of $2n = 15$. This species seems most closely related to *Arabis depauperata*.

24. **Arabis depauperata** Nelson & Kennedy, Proc. Biol. Soc. Wash. 14: 35. 1906; Summit Mt. Rose, Washoe Co., Nevada, *P. B. Kennedy 1167* (ISOTYPE UC!). *Arabis lemmonii* var. *depauperata* (Nelson & Kennedy) Rollins, Rhodora 43: 384. 1941.

Arabis interposita Greene, Leaflets Bot. Obs. & Crit. 2: 78, 79. 1910; Ashland Butte, Siskiyou Mts., and Crater lake, Cascade Mts., southern Oregon, *Wm. C. Cusick 2970* (LECTOTYPE US!, plant second from left; ISOLECTOTYPE GH!, plant on left). *Arabis divaricarpa* var. *interposita* (Greene) Rollins, Rhodora 43; 378. 1941.

Arabis acutina Greene, Leaflets Bot. Obs. & Crit. 2: 82. 1910; On an open rocky slope, Mount Thielson, Cascade Mts., Oregon, *F. V. Coville & E. I. Applegate 434* (LECTOTYPE US!; ISOLECTOTYPES RM!, US!).

Arabis bracteolata Greene Leaflets Bot. Obs. & Crit. 2: 73. 1910; Northwestern Wyoming, *J. N. Rose 1893* (HOLOTYPE US!).

Arabis nubigena Macbr. & Payson, Contrib. Gray Herb 49: 62. 1917; Gravelly flat, alt. 9000 ft., Smoky Mts., Blaine Co., Idaho, *J. F. Macbride & E. B. Payson 3772* (HOLOTYPE GH!; ISOTYPES UC!, US!, RM!). *Arabis microphylla* var. *nubigena* (Macbr. & Payson) Rollins, Res., St., State Coll. Wash. 4: 40. 1936.

Arabis microphylla var. *thompsonii* Rollins, Rhodora 43: 429. 1941. Kittitas Co., Washington, alpine meadows of Table Mt., 5000 ft., *J. W. Thompson 9266* (HOLOTYPE GH!; ISOTYPES NY!, US!).

DISTRIBUTION. On rocky alpine slopes in southern British Columbia. I have seen specimens from Montana, Nevada and California. It almost certainly also occurs in Idaho, Washington and Oregon.

BIOLOGICAL NOTES. *Arabis depauperata* contains diploid plants based on $x = 7$ (Table 1). It seems most closely related to *A. microphylla.*

25a. **Arabis holboellii** Hornem. var. **holboellii,** *Arabis holboellii* Hornem., Fl. Dan. 2: 5. 1827; plate 1879.

Arabis holboellii var. *tenuis* Böcher, Svensk Bot. Tidskrift 48: 38. 1954; ex Ilwdlinguaq sinus Søndre Strømfjord, Greenland, *T. Böcher, 22, 5, 1951* (HOLOTYPE C, not seen).

DISTRIBUTION. Open habitats in Greenland.

25b. **Arabis holboellii** var. **consanguinea** (Greene) G. Mulligan, *comb. nov.* Based on *Arabis consanguinea* Greene, Pittonia 4: 190. 1900; Los Pinos, southern Colorado, 7000 ft., *C. F. Baker 342* (HOLOTYPE ND!; ISOTYPES ND!, RM!, US!).

DISTRIBUTION. Open grassland and scrub in Alaska (rare), Yu-

kon (rare), Saskatchewan (rare), Alberta, British Columbia, Washington, Oregon, California, Nevada, Colorado and Utah.

25c. **Arabis holboellii** var. **retrofracta** (Graham) Rydberg, Contrib. U.S. Nat. Herb. 3: 484. 1896. Based on *Arabis retrofracta* Graham, Edinb. Phil. Journ. 345. 1829; Rocky Mountains, Palliser's Brit. N. Am. Expl. Expedition, *E. Bourgeau, 1858* (PROVISIONAL LECTOTYPE GH!, chosen by Hopkins, 1937 and confirmed by Rollins, 1941; no specimen referred to in Graham's original description and there is no suitable material in the Royal Botanic Garden in Edinburgh).

Arabis rhodantha Greene, Pittonia 3: 155. 1897; Above Empire, Colorado, *E. L. Greene, 1875* (HOLOTYPE ND!, sheet 6327; ISOTYPE ND!, left specimen on sheet 6328).

Arabis tenuis Greene, Pittonia 4; 189. 1900. On mountains, 2000 ft. alt., W. Klickitat, Washington, *W. N. Suksdorf 15* (HOLOTYPE ND!; ISOTYPE GH!).

Arabis lignipes A. Nelson, Bot. Gaz. 30: 191. 1900; Madison River, Yellowstone National Park, *A. & E. Nelson 5505* (LECTOTYPE RM! by Rollins, 1941; ISOLECTOTYPE RM!).

Arabis caduca A. Nelson in Coulter & Nelson, New Man. Bot. Rky. Mts. 229. 1909; Woods Creek, Wyoming, *A. Nelson 2584* (HOLOTYPE RM!).

Arabis polyantha Greene, Leaflets Bot. Obs. & Crit. 2: 80. 1910; Along R.R. track at Rock Island, Washington, *K. Whited 1043* (HOLOTYPE US!).

Arabis macdougalii Rydberg, Bull. Torr. Bot. Club 3: 326. 1912; Old Sentinel, near Missoula, Montana, *MacDougal 191* (HOLOTYPE NY!; ISOTYPES NY!, US!).

Arabis retrofracta var. *multicaulis* B. Boivin, Can. Field-Nat. 65: 17. 1951; left bank of Malique R. at Fish Hatchery, Jasper National Park, *G. H. Turner 5086* (HOLOTYPE DAO!).

DISTRIBUTION. Grass slopes, talus, benches, roadsides, hillsides and many other open habitats in Alaska, Yukon, Mackenzie District, Quebec (rare), Ontario (rare), Manitoba, Saskatchewan, Alberta, British Columbia and southward. United States specimens were seen from Michigan, North Dakota, South Dakota, Montana, Wyoming, Colorado, Utah, Idaho, Washington, Oregon, Nevada and California.

25d. **Arabis holboellii** var. **secunda** (Howell) Jepson, Man. Fl. Pl. Calif. 430. 1925. Based on *Arabis secunda* Howell, Erythea 3: 33. 1895; Mount Adams, Washington, *T. Howell 1487* (HOLOTYPE ORE!; ISOTYPES NY!, US!).

Arabis collinsii Fernald, Rhodora 7: 32. 1905; Limestone—conglomerate cliffs and ledges, island—headland east of Baptiste Michaud's, Bic, Rimouski Country,

Quebec, *J. F. Collins & M. L. Fernald July 16 & 18, 1904* (HOLOTYPE GH!; ISOTYPES CAN!, DAO!, GH!, MT!). *Arabis holboelii* var. *collinsii* (Fernald) Rollins, Rhodora 43: 445. 1941. *Arabis retrofracta* var. *collinsii* (Fernald) B. Boivin, Can. Field-Nat. 65; 17. 1951.

DISTRIBUTION. Prairie, grasslands, sand, and rocky areas in Alaska, Yukon, Mackenzie District, Quebec (rare, but common in Gaspé), Ontario (rare), Saskatchewan, Alberta, British Columbia and southward. Specimens were seen from Washington, Idaho, Montana and Utah. It probably occurs elsewhere in the western United States.

BIOLOGICAL NOTES. *Arabis holboellii* is nearly as widespread as *A. divaricarpa* and is certainly more abundant within its range. I have recognized four taxa of *A. holboellii* at the varietal level, all of these appearing to contain sexual and apomictic diploids and apomictic triploids, based on $x = 7$ (Table 1). I suspect that the sexual diploids are self-compatible.

26. **Arabis boivinii** G. Mulligan, *sp. nov.*

Arabis divaricarpa var. *dechamplainii* B. Boivin, Naturaliste Can. 94: 645. 1967; Cap au Cobeau, Bic, rochers maritimes calcaires, *A. A. De Champlain 1577* (HOLOTYPE DAO!; ISOTYPE MT!).

Arabis boivinii ab A. lignifera different inflorescentia leviter secunda, trichomatibus in foliorum radicalium paginis inferioribus plus quam 0.25 mm latis et habitu bienni vel breviter perenni.

Arabis boivinii differs from *Arabis lignifera* by its slightly secund inflorescence, its wider trichomes on undersurfaces of caudex leaves (i.e., more than 0.25 mm wide), and its biennial or short-lived perennial growth habit.

The holotype specimen in the herbarium of Agriculture Canada, Ottawa, is named after Bernard Boivin, 1916–1985 (see tribute to Boivin by Cody and Cayouette, 1986). Saskatchewan, District de Maple Creek, Carmichael, 10 milles au sud, Monts Cyprès écorre de la coulèe du ruisseau Bone, inflorescence seconde ou parfois distique, *B. Boivin & J. Alex 9738,* 8 juillet, 1952 (HOLOTYPE DAO!; ISOTYPE MT!). *Arabis divaricarpa* A. Nels. var. *hemicylindrica* B. Boivin, Amer., Midl. Nat. 54: 510. 1955 (same type as *A. boivinii*).

Biennial or short-lived perennial with a simple, compact caudex; stems erect, usually single, simple to few branched, 30 to 60

cm high; cauline leaves entire to rarely few toothed, glabrous to pubescent, sessile, mostly strongly sagittate-clasping stems, narrowly lanceolate, 1.0 to 2.5 cm long, 3 to 5 mm wide; caudex leaves entire to few toothed, compact, 1.5 to 2.0 cm long, 3 to 6 mm wide, blades lanceolate, slender petiolate; lower surfaces of caudex leaves with sparse to dense sessile to short-stalked, branched, 3- to 4-parted trichomes mostly 0.35 mm wide; inflorescences semisecund, open; fruiting pedicels arcuate-spreading to arcuate-descending, 3 to 9 mm long; siliques slightly descending to strongly descending, straight to slightly arcuate, 4.0 to 6.5 cm long, 1.5 to 2.0 mm wide, style rudimentary; seeds mostly in 1 row, brownish, oval, 1.75 mm long, 1.25 to 1.5 mm wide, narrowly winged at apex, cotyledons accumbent.

DISTRIBUTION. Dry prairie and hills of southern Saskatchewan, Montana and South Dakota and probably elsewhere on the plains of the United States; disjunct eastwards to limestone cliffs and ridges of Cap aux Corbeaux, Rimouski County, Quebec.

BIOLOGICAL NOTES. *Arabis boivinii* is a triploid based on $x = 7$ (Table 1). Morphologically it seems somewhat intermediate between *Arabis holboellii* and *Arabis divaricarpa.* Although both of these taxa occur within the range of *A. boivinii,* there is no evidence that it has resulted from recent hybridizations. I am treating it as a species resulting from the ancient hybridization of *A. holboellii* and *A. divaricarpa.* Rollins (1983) has suggested that *A. divaricarpa* itself is probably of ancient hybrid origin.

REPRESENTATIVE SPECIMENS. CANADA. **Quebec:** Cap aux Corbeaux, Comtè de Rimouski, sur le conglomerat nu, *Rousseau 26440* (DAO, MT); Point aux Corbeaux to Cap Caribou, Bic, limestone and limestone-conglomerate ridges, *Fernald & Collins 1061* (CAN). **Saskatchewan:** Cypress Hills, side hill on Bald Butte, *Budd 2005* (SASK); Cypress Hills Park, open plateau, occasional, *Breitung 4401* (MT); 12 miles south of Indian Head, dry south-facing knoll, *Jones 784* (SASK). UNITED STATES. **Montana:** Cascade Co., 3.8 miles south of Neihart, fresh road cut, clay-gravel soil, *Mosquin & Gillett 5219* (DAO). South Dakota: Lawrence Co., 2 miles north and ½ mile west of Savoy, steep south facing eroding slopes, *Mosquin & Mulligan 5157* (DAO).

27. **Arabis lignifera** A. Nelson, Bull. Torr. Bot. Club. 24: 123. 1899; Green River, Sweetwater Co., Wyoming, *A. Nelson 4711* (HOLOTYPE RM!; ISOTYPES GH!, MO!).

Arabis densicaulis A. Nelson, Bot. Gaz. 30: 190. 1900. In rocky exposed places on an abrupt slope, Undine Falls, Yellowstone National Park, *A. & E. Nelson 5680* was designated as the type for both *A. densicaulis* and *Arabis elegans* A. Nelson (Bot. Gaz. 30: 191. 1900). However, the specimens in RM and MO fit the description of *A. densicaulis* not *A. elegans*. A note on the isotype of *A. densicaulis* in RM, written by C. L. Porter '51, states that "also cited as a type of *A. elegans* A. Nels., Bot. Gaz. 30: 192, 1900 but this was an error for No. 6939."

Arabis subserrata Greene, Leaflets Bot. Obs. & Crit. 2: 79. 1910; Ellensburg, Washington, *K. Whited 321* (HOLOTYPE US!; ISOTYPE WS!).

DISTRIBUTION. Open rocky areas in northwest corner and in southern British Columbia and southward. It also grows in Idaho and Wyoming to Colorado and west to Nevada (Rollins, 1993b).

BIOLOGICAL NOTES. *Arabis lignifera* contains diploid plants with the base number $x = 7$ (Table 1).

28. **Arabis sparsiflora** Nuttall in T.&G., Fl. N. Am. 1: 81. 1838; Forests of Rocky Mountains, towards sources of Oregon (LECTOTYPE PH!, specimen on extreme right of herbarium sheet).

Arabis sparsiflora var. *arcuata* (Nuttall) Rollins, Res. Studies State Coll. Wash. 5: 26. 1936. Based on *Streptanthus arcuatus* Nuttall in T.&G., Fl. N. Am. 1: 77. 1836; Santa Barbara, *Nuttall* (HOLOTYPE PH!; ISOTYPE GH!).

Arabis sparsiflora var. *peramoena* (Greene) Rollins, Res. Studies State Coll. Wash. 5: 26. 1936. Based on *Arabis peramoena* Greene, Feddes Repertorium 5: 242. 1908; Dry sandy soil of Willow Creek, Malheur Co., Oregon, purple showy flowers, *W. C. Cusick 2309* (ISOTYPES NY!, RM!, US!).

Arabis campyloba Greene, Pittonia 4: 192. 1900; Near Yreka, California, *E. L. Greene, April & May 1876* (HOLOTYPE ND!).

Arabis polystricha Greene, Leaflets Bot. Obs. & Crit. 2: 72. 1910; Dry hill near near Yreka, Siskiyou Co., California, *Butler 723* (HOLOTYPE ND!; ISOTYPES ND!, P!, RSA-POM!, UC!).

Arabis arcoidea A. Nelson, Bot. Gaz. 53: 220. 1912; Loamy creek banks among hills, altitude 2200, near Plymouth, Canyon County, Idaho, *J. F. Macbride 87* (HOLOTYPE RM!; ISOTYPES GH!, RM!).

Arabis sparsiflora var. *californica* Rollins, Rhodora 43: 402. 1941; California, on dry hills, near Campo, San Diego County, *L. Abrams 3563* (HOLOTYPE GH!).

DISTRIBUTION. Occurs in sagebrush and on dry benches in southern British Columbia (only near Penticton), Idaho, Oregon, Arizona, Nevada, California and Washington.

BIOLOGICAL NOTES. One diploid population, with the base number $x = 7$, growing in Arizona was apparently sexual, whereas another was probably apomictic (Table 1). Raven et al. (1965)

and Böcher (1969) reported $2n = 22$ for plants from California. Böcher observed the configuration of 7II + 8I at metaphase I. It appears that sexual diploids and apomictic diploids and deviant triploids, based on $x = 7$, occur in this species.

29. **Arabis columbiana** Macoun, Mac. Cat. 5: 304. 1890; Gravel, Yale, B.C., *Macoun, May 17th, 1889* (LECTOTYPE CAN!; ISOLECTOTYPE GH!). *Arabis sparsiflora* var. *columbiana* (Macoun) Rollins, Rhodora 43: 405. 1941.

Arabis sparsiflora var. *subvillosa* Rollins, Rhodora 43: 403. 1941. Based on *Arabis arcuata* Gray var. *subvillosa* Watson in Gray, Syn. Fl. N. Am. 1: 164. 1895; Pulman, Washington, *C. V. Piper, May 20, 1894* (HOLOTYPE GH!).

Arabis elegans Nelson, Bot. Gaz. 30: 192. 1900; Undine Falls, Yellowstone National Park, *A. & E. Nelson 6939* (LECTOTYPE RM!).

Arabis stokesiae Rydb., Fl. Rocky Mts. 361. 1918; Parley's canyon, Wahsatch Mts., alt. 5000 ft., *S. G. Stokes, June 8, 1901* (HOLOTYPE US!; ISOTYPE GH!, NY!).

DISTRIBUTION. Grasslands, sagebrush, rock outcrops, talus slopes, and open woods in Yukon, British Columbia, Washington, Idaho, Oregon, California, Nevada and Utah.

BIOLOGICAL NOTES. It appears that sexual and apomictic diploids and apomictic triploids, based on $x = 7$, occur in *A. columbiana* (Table 1).

30. **Arabis pinetorum** Tidestrom, Proc. Biol. Soc. Wash. 36: 182. 1923; In coniferous forest north of Glenbrook, along Lake Tahoe, Nevada, elev. 1890 meters, *I. Tidestrom 10387* (HOLOTYPE GH!). *Arabis holboellii* var. *pinetorum* (Tidestrom) Rollins, Rhodora 43: 447. 1941. *Arabis divaricarpa* var. *pinetorum* (Tidestrom) B. Boivin, Can. Field-Nat. 65: 16. 1951.

DISTRIBUTION. Open slopes, dunes and prairie in Alaska, Yukon, Mackenzie District, Manitoba, Saskatchewan, Alberta and British Columbia. Specimens were seen from North Dakota, Utah, Wyoming, Nevada and California. It undoubtedly occurs elsewhere in the western United States.

BIOLOGICAL NOTES. Plants with the somatic chromosome numbers of 14, 13 + 2B and 21 occur in *A. pinetorum* (Table 1). One of the sites, in California, had diploid plants with an irregular meiosis. It, therefore, seems likely that apomicts, based on $x = 7$, occur both at the diploid and triploid level.

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